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THE ROLE OF SEXUAL SELECTION IN DETERMINING OVERALL
MATING PATTERNS AND MATE CHOICE
IN CHUM SALMON¹

by

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COMPLETION REPORT

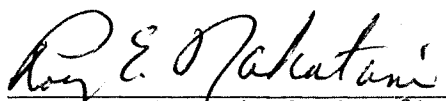
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ABSTRACT

THE ROLE OF SEXUAL SELECTION IN DETERMINING OVERALL
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By Steven L. Schroder

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The influence of sexual selection on overall mating patterns and mate choice in chum salmon demes was examined by observing fish in an experimental stream and viewing chamber. Males remained sexually active throughout most of their spawning ground residency ($\approx$ 10 to 14 days) while females often finished spawning within two days after establishing a territory. Consequently, the Operating Sex Ratio (OSR) in most spawning communities is skewed in favor of females. Such skewed sex ratios strongly affect overall mating patterns. When the OSR within a deme was ≤ 1 , every male was successful. However, as OSR values increased only the strongest or largest males spawned successfully.

To circumvent this type of intrasexual competition subdominant males positioned themselves downstream of mating pairs and attempted to "steal" fertilizations. At low OSRs the occurrence of such "satellite" males was close to zero but it rose asymptotically to 20% at higher OSRs. The number of satellites associated with a pair remained relatively constant (1 to 2) at the OSRs examined. However, the percentage of pairs within a deme accompanied by satellites increased in a linear fashion as male competition for females escalated. Gametic success of

satellite males as measured by electrophoresis showed that satellite males may fertilize 20 to 25% of the eggs deposited during a spawning.

Socially dominant males usually had vertical bars while subdominant ones and females generally possessed a single horizontal stripe. Videotapes made of single pairs revealed that females were "aware" of both the color pattern and relative size of their consorts. When courted by relatively "small" males or those with stripes females slowed down nest construction.

Intrasexual competition for egg burial sites occurred when ≤ 1.66 m² of spawning area was available per female. The size of a female did not influence her ability to successfully establish a territory. Territory size was influenced only by the number, and not the size, of territorial females within a spawning community. Generally the greater the competition for space the smaller the area a female could successfully hold.

Males did not find large females more "attractive" than small ones. However, they preferred females that were engaged in nest digging over those that were quiescent or guarding their nests. Apparently, the impossibility of predicting the number of eggs a female will deposit, the size of those eggs, the quality of the subsequent young, and the costs incurred by being selective (time lost by searching) have forced males to adopt the strategy of attempting to fertilize as many eggs as possible.

Since females exhibited a behavioral preference for relatively large mates, three artificial crosses were made to determine if paternal traits could be linked to early progeny performance. The families produced from these crosses did differ in their viability, growth rates, etc., but none of these differences could be associated with any observable paternal traits. One possible explanation for the observed feminine preference is that within the genus Oncorhynchus males tend to mature at the same age as their fathers. Consequently, by mating with large and presumably old males a female increases the probability that her sons will have greater access to females than if she were nonselective.

Unlike several other studies dealing with mate selection in Pacific salmon I did not observe an innate preference for similar appearing mates. Instead, pairing in this species is based upon the outcomes of masculine intrasexual competition and feminine epigamic selection.

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CHAPTER I. INTRODUCTION

The reproductive activities of Pacific salmon (Oncorhynchus spp.) have fascinated investigators for almost a hundred years. Yet, at present little information is available regarding the mating systems and sexual preferences occurring in breeding aggregations of these fishes. Clearly, the pattern of mate selection within a breeding population of salmon is a reflection of many individual choices made by males and females. To fully understand why salmon select mates the way they do, we have to link this behavior with their potential fitness; i.e., how does mate choice influence an individual's ability to perpetuate its genes.

Two processes are involved whenever mate choice occurs, species identification, and intraspecific mate selection. I have concentrated on the second; how and why mates are chosen within breeding aggregations of chum salmon (O. keta). Who spawns with whom is basically determined by the balance existing between intrasexual and epigamic selection, the two components of sexual selection. This balance can be affected by the mating system existing within each breeding population. In this section, I define mating systems and discuss the environmental and phylogenetic factors that influence their existence. Secondly, I discuss the roles that sexual preferences and intrasexual competition play in mate choice. Next, mating patterns and mate choice are differentiated from one another. Finally I review two previous studies dealing with mate

selection in salmon and present questions arising from these studies. The remainder of the dissertation deals with their solution.

Operational Definitions of Polygamy,
Monogamy, and Promiscuity

Mating systems may be thought of as general behavioral strategies used to acquire mates and produce young. Each strategy is defined by how mates are obtained, the number acquired per season, the absence or presence of pair bonds, and how each sex takes care of its young (Emlen and Oring 1977). Polygamy and monogamy are the two basic mating strategies available to diploid animals (Emlen 1973; Wilson 1975). Polygamy occurs when one or both sexes obtain more than one mate, either simultaneously or in succession during a breeding season. I identify three types of polygamy; polygyny, where males acquire multiple mates; polyandry, where females do; and multiple polygamy where both sexes obtain more than one mate (for a detailed ecological separation of polygamy, see Emlen and Oring 1977). Each type of polygamy can be further defined by whether prolonged pair bonds occur between the mated pairs. If the pair bond does not continue beyond copulation then the sexual relationship between the male and female is promiscuous (Emlen 1973). In promiscuous and nonpromiscuous polygamy one sex usually protects and sometimes nourishes the young if parental care is required. Two types of monogamy have been identified; obligate and facultative (Kleiman 1977 as cited by Ralls 1977). In obligate monogamy both sexes tend the young and thus a permanent pair bond exists at least through the rearing of one brood (Emlen 1973; Wilson 1975). In facultative monogamy the relationship

between the sexes is promiscuous but only one mate can be acquired because of environmental or phylogenetic factors.

The Influence of Phylogenetic and Environmental Factors on Mating Systems

Two factors will influence the type of mating system that will occur in a breeding population. Certain phylogenetic propensities, besides anisogamy, will tend to promote the occurrence of polygamous mating systems. For example, tendencies to reduce parental care either by the production of young that are entirely self-sufficient or nearly so (most fishes, amphibians, arthropods, lower invertebrates, and the majority of birds with precocial young), or the predisposition of one sex to assume most of the parental care (e.g., mammals) will sometimes allow one and rarely both sexes a chance to remate. Additionally, short periods of courtship (promiscuity) and prolonged periods of sexual activity in one or both sexes will also provide the animals with time to search for additional mates (Emlen and Oring 1977; Wilson 1975; Trivers 1972; Orrians 1969). By themselves, such predispositions will not lead to polygamy, but merely make it easier for one or both sexes to capitalize on the "polygamy potential" of their breeding environment (Emlen and Oring 1977).

The polygamy potential in any environment depends "...on the degree to which multiple mates, or resources critical to gaining multiple mates, are economically defendable" (Emlen and Oring 1977, p. 215). When important resources (food, nest sites, etc.) are evenly distributed there is little opportunity for resource monopolization. Members of the

breeding aggregation will tend to disperse and consequently the opportunities for acquiring multiple mates will be low. On the other hand, if such resources are highly clumped the "polygamy potential" may be high, for some individuals might be able to control higher quality or larger portions of the needed resources (Emlen and Oring 1977).

The benefits (in terms of potential fitness) derived from defending a resource are associated with the temporal arrival and sexual receptivity of potential mates. If, for example, all the females in a population become sexually receptive at once and for a short period of time, then the likelihood of a male monopolizing more than one female becomes very small. This occurs because by the time a male locates a female and inseminates her eggs, few additional partners would be available (Emlen and Oring 1977). Conversely, if female arrival were more prolonged and males were to remain sexually active during this period, then opportunities for multiple mate monopolization would increase (Emlen and Oring 1977).

Other environmental factors, such as super abundance of renewable food (Orrians 1969; Verner and Willson 1966; Verner 1964) and heavy predation at breeding sites (Orrians 1969; Wilson 1975) have also been suggested as increasing the probability of polygamy. The important point is, that as environmental conditions change, the economic feasibility of certain behavioral strategies also shift. This means that different mating systems may occur in separate populations of the same species (Emlen and Oring 1977).

Sexual Selection: The Distinction Between Epigamic and Intrasexual Selection

Darwin felt that sexual selection possessed two distinct components, one was concerned with the "power to conquer other males in battle" (intrasexual selection) and the other (epigamic selection) with "the power to charm the females" (Huxley 1938; Fisher 1958, Wilson 1975; Mayr 1976). Both of these operational definitions have been slightly revised since Darwin first proposed them, but field data have supported their importance in animal populations. Yet, in practice it is usually difficult to separate the impact each may have on mate choice since attributes that "charm" one sex may repulse the other.

Intrasexual Selection

Intrasexual selection takes place when members of the same sex attempt to nullify previous matings by sexual rivals, exclude one another from mates, or from resources essential for successful reproduction. Both sexes engage in this type of competition and it may occur before and after copulation. Wilson (1975) has suggested that four types of precopulatory competition exist--competition in finding mates, excluding others from territories, obtaining dominance in permanent social groups, and obtaining dominance during courtship. Even after an individual successfully copulates, intrasexual competition can still occur. Sperm competition (external fertilizers) and displacement (internal fertilizers) may happen, abortions can be induced (e.g., the so called "Bruce" effect in mice) and offspring may be killed (Wilson 1975). Various strategies have evolved to prevent this kind of genetic

usurpation. Males may insert mating plugs or place repellents on their mates. Other species have prolonged periods of copulation, or "passive phases" where one suitor guards a mate by staying attached or in close proximity to it. (Wilson 1975; Abele and Gilchrist 1977).

In polygamous mating system, intrasexual competition will play an important role in determining mate choice and mating frequency. The intensity of intrasexual competition can be assessed by dividing the quantity of the limiting resource (mates, territories, etc.) by the number of individuals competing for it. An important ratio of this type is the number of sexually active males to fertilizable females. This Operating Sex Ratio (Mathisen 1955; Potter 1976a and 1976b; Emlen and Oring 1977) reflects any imbalances in a population that may lead to intrasexual competition. The more skewed the Operating Sex Ratio the greater the variance in the reproductive success of the "limited" or competing sex. However, competition among members of the same sex for mates or for resources that will attract mates is only one half of sexual selection.

Epigamic Selection

Epigamic selection (Huxley 1938) can also influence mate choice in monogamous mating systems and in polygamous ones when the Operating Sex Ratio is not heavily skewed. Such selection occurs when one or both sexes choose their mates among many alternates on the basis of showiness, athletic prowess or the possession of other specific characteristics (Emlen 1973; Willson 1975). These phenotypic traits may not be

universally desirable, i.e., different individuals within a breeding population may have dissimilar mate preferences.

Who Should Be Choosy. In most species mate choice falls primarily on the female because the cost of making a mistake (infertile or nonviable offspring) is much higher for her than it is for a male (Emlen 1973; Mayr 1976). This occurs because sperm is less costly (per gamete) to produce than eggs or maternal care. Thus females should be choosy about selecting their mates when they provide their young with large, nutrient-rich eggs or spend time and energy in tending them (Orians 1969; Emlen 1973; Alcock 1975; Williams 1975). This imbalance in the parental investment¹ ledger has caused males and females to evolve different behavioral strategies while attempting to maximize their genetic fitness (Triver 1972; Williams 1975). Williams (1975) suggests that in most species, males should take the active role in courtship, have an inclination towards promiscuity, be less discriminating toward possible mates than females, and be antagonistic toward potential sexual rivals. In essence, the optimal male strategy is often to fertilize as many eggs as possible. Consequently, males are usually subjected to both types of sexual selection to a much greater extent than females (Emlen 1973).

¹Trivers (1972, p. 139) has defined parental investment "... as any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence, reproductive success) at the cost of the parent's ability to invest in other offspring. So defined, parental investment includes the metabolic investment in the primary sex cells (and also) refers to any investment (such as feeding or guarding the young) that benefits the young. It does not include effort expended in finding a member of the opposite sex or in subduing members of one's own sex in order to mate with a member of the opposite sex..."

The only genetic advantage a female would obtain by having her eggs fertilized by more than one male would be to increase the genetic diversity of her offspring. But as Williams (1975) points out, nearly all the genetic diversity possible from sexual reproduction can be obtained by mating with just a few males. Thus females are usually less concerned about the quantity of mates they acquire than about the quality of the males that fertilize their eggs (Fisher 1958; Williams 1975).

Types of Mate Choice and Their Possible Origins. Theoretically a female should choose only males of her own species that are mature and sexually competent. Moreover, she should prefer males that have demonstrated they can survive (older over younger males), reproduce (healthy over sickly or undernourished ones), and who possess genes that complement her own. In those species where paternal care occurs additional factors relating to the willingness and ability of the male to provide care will also be important (Trivers 1972).

Frequency-dependent mate choice. Field and laboratory studies have shown that subtle female preferences occur in many animal species (Trivers 1972). Mates can be chosen on the basis of phenotype rarity or novelty. Such frequency-dependent mating has been observed in insects, e.g., Drosophila spp. (Ehrman 1966, 1970a, 1970b; Spiess 1968; Petit and Ehrman 1969), Tribolium castaneum (Shinnock 1970), and Mormoniella vitripennis (Grant et al. 1974) and in several vertebrate species, e.g., the guppy (Poecilia reticulata) (Farr 1977) and the Greylag goose (Lorenz as quoted by Ehrman 1966).

The behavioral mechanism permitting this type of discrimination is most likely habituation (Ehrman and Spiess 1969). Farr (1977) presents data showing that female guppies become less receptive to sexual advances when the male possesses a frequently seen color morph. Thus when a female is confronted by a "novel" appearing conspecific male she is more likely to accept him as a mate than one with a more commonly seen color pattern. A similar type of mechanism probably is responsible for the "rare male advantage" in Drosophila populations. In this case females become habituated to prevalent pheromone odors rather than color patterns (Averhoff and Richardson 1975).

It has been hypothesized that the ultimate factor responsible for frequency-dependent mate choice deals with the genetic diversity of the offspring. If a female mates with a novel appearing male (assuming she is of the prevalent type) the likelihood that she shares many genes in common with her mate should be small. Consequently, her offspring will have a greater amount of genetic diversity than they would under random mating (Farr 1977). Such genetic heterozygosity allows for a great deal of genetic flexibility and is adaptative under some circumstances (Ayala et al. 1974).

Disassortative mate choice. In some instances females may choose their mates in a disassortative fashion. This occur when females prefer males that differ from them in one or more phenotypic traits, but do not base their decisions on the rarity of the male phenotype. Sexual preferences of this type have been observed in mammals (Yanai and

McClearn 1972, 1973a, 1973b), birds (Lowther 1961; Jehl 1970), fish (Borowsky and Kallman 1976), and in several species of insects (Sheppard 1952; Wallace 1968). Sometimes such choices are based on imprinting as Yanai and McClearn (1972, 1973a) demonstrated in the mouse (Mus musculus domesticus). However, in most cases the behavioral mechanisms employed by the female are unknown. By choosing mates in this manner the genetic heterozygosity of a female's offspring is again greater than that which would occur if mate choice were random.

Assortative mate choice. The propensity for females to prefer males possessing phenotypic traits similar to themselves also occurs. Like the other types of female preference previously discussed, assortative mate choice can be based on discrete (e.g., deafness in humans, color, odor, etc.) or continuous phenotypic traits (weight, length, and so on). Cooke et al. (1972, 1976) showed that snow geese (Anser caerulescens) having similar color patterns preferentially mated with one another. They found that such choices occurred because the young imprinted on the plumage color of their parents and siblings. Midas cichlids (Cichlasoma citrinellum) with similar color patterns also tend to form pairs (Barlow and Rogers 1978). Here it was found that female choice was influenced by her parents' color, her own color, and possibly by male behavior. In these instances, and many others (see Lill, 1968a, 1968b; Wilson 1975) the original, if not the present purpose of assortative mate choice is most likely to prevent genetic introgression.

Another possible explanation for assortative mate choice is that copulation and subsequent fertilization is enhanced when certain size ratios exist between mated pairs. In the American toad (Bufo americanus) females were observed selecting males slightly smaller than themselves (Licht 1976). The call notes of the males reflect their size and apparently females discriminate among them on this basis. Evidently, an optimum size ratio between the pair is needed to ensure successful amplexus. A preference for mates with similar body size was also observed in the pupfish (Cyprinodon sp.) by Kodric-Brown (1977). In her study evidence is presented that indicates neither male preference nor intra-sexual competition among females for males possessing "good oviposition" sites were responsible for this phenomenon. Kodric-Brown speculates that size selection of mating partners in fishes may occur because it allows the spawning sequence to progress smoothly and possibly prevents injury to females from larger, sexually aggressive males. Additional examples of this type of female preference can be found in other species as well (e.g., see Parsons 1965, 1967).

Large body size. Large males may be preferred by females even when they do not possess territories or provide any kind of paternal care to their offspring. Such males are older or have faster growth rates and both are signs of vigor and perhaps of a superior genotype. Old age is post facto evidence of survival value while rapid growth is advantageous in both larval stages and in attaining early maturity (Wilbur et al. 1978). Additionally, if there is a positive correlation between fecundity and female body size (e.g., in many fishes and

amphibians), a female should choose a male that will confer a large body size on her daughters. Moreover, her sons would also benefit since large size would give them a mating advantage over smaller rivals (Wilbur et al. 1978). Likewise, males should also prefer large females in these species because they possess more and possibly larger eggs (Williams 1975).

Social status. A female may also maximize the probability that she will produce offspring of high quality by choosing males that have demonstrated their ability to survive and accrue resources (Trivers 1976). High ranking males have probably illustrated their superiority in both of these categories by simply dominating their rivals. Therefore, in some cases females may use the social position of a male as a basis for mate choice. There are four ways in which male status might be detected. First, in some species certain color patterns are associated with dominance. For instance, high ranking males are black in the Gila top minnow (Poeciliopsis occidentalis), dark blue in pupfish and so on (Constantz 1975; Kodric-Brown 1977). Second, in almost all the species that form leks, a few territories can only be held by the most dominant males within a particular breeding population. Hence, by assessing the location of a male, a female can discern his relative social status (Wilson 1975). Third, in some species only dominant males can perform particular types of motor activities. For example, in spawning populations of the Fallfish (Semotilus corporalis) a few dominant males dig shallow depressions in a streambed. After the males finish digging they search the surrounding substrate for stones which they place into their

newly created nests. Gravid females and subordinate males cluster around these sites while nest construction takes place. But the females will only spawn in these areas when the dominant male deposits a stone or rushes over the gravel mound of his nest (Ross and Reed 1978). Fourth, a female can determine a male's social status by activating any existing dominance hierarchy. Cox and LeBoeuf (1977) describe how this occurs in elephant seals (Mirounga angustirostris). This species has breeding aggregations consisting of many females guarded by several large bulls or "beachmasters." Weaker or younger males station themselves at the peripheral edges of these "harems" and attempt to mate with any females that become available. Females, while in early estrus, physically and vocally protest any attempt at copulation. This protest behavior "literally wakes up sleeping males" and prompts them to compete among themselves to copulate or prevent other males from copulating with the female. By this mechanism females are usually assured of mating with the "best" male in the harem. Additional examples of this behavior are provided by Cox and LeBoeuf and they further suggest that female incitation of male competition should commonly occur in many polygamous species.

Other forms of mate choice. Lastly, the performance of courtship movements such as dances or other displays (Wilson 1975) and the brightness or form of the breeding dress (Noble 1938; Huskins et al. 1961, as cited by Gandolfi 1971) have also been mentioned as other characteristics a female may use to discriminate among potential mates. To

help visually conceptualize all of the various types of mate choice mentioned I have diagrammatically illustrated them in Fig. 1.

The Difference Between Mate Choice and Overall Mating Patterns. The above observations indicate that the number of mates chosen is influenced by environmental and phylogenetic factors, while who is chosen is usually affected by sexual selection. However, the simple resemblance, dissimilarity, etc. of phenotypic traits among mated pairs do not by themselves reflect how choices are made. For instance, the reasons that members of a pair may resemble one another may have nothing to do with a female or male preference for phenotypically similar mates. Instead, temporal, spatial, and mechanical isolation, incidental phenotype similarity, intrasexual competition, and similar genetic backgrounds among the mating individuals may cause an assortative mating pattern.²

²There is some confusion as to what assortative, disassortative, frequency-dependent, random, and other mating patterns and choices represent. I feel that an assortative mating pattern occurs when individuals with similar phenotypes form pairs regardless of how this happens. On the other hand, assortative mate choice only occurs when individuals prefer similar appearing mates. This distinction is also applicable to the other types of mating patterns and choices mentioned above. Population geneticists add one more restriction to these definitions. They feel that an assortative mating pattern only occurs when the gene but not genotype frequencies in the parental and offspring generation remain the same after mating (Taylor 1975). When both gene and genotype frequencies are similar, then mating has been random. If a change in the gene frequency does occur then mating has been selective. There are probably very few populations where selective mating does not occur. Nevertheless, the heuristic value of a term like assortative mating is great enough to use it without this last restriction. Thus, no genetic connotations are implied when I call a mating pattern assortative, disassortative, and so on.

SOME COMMON
TYPES OF MATE CHOICE

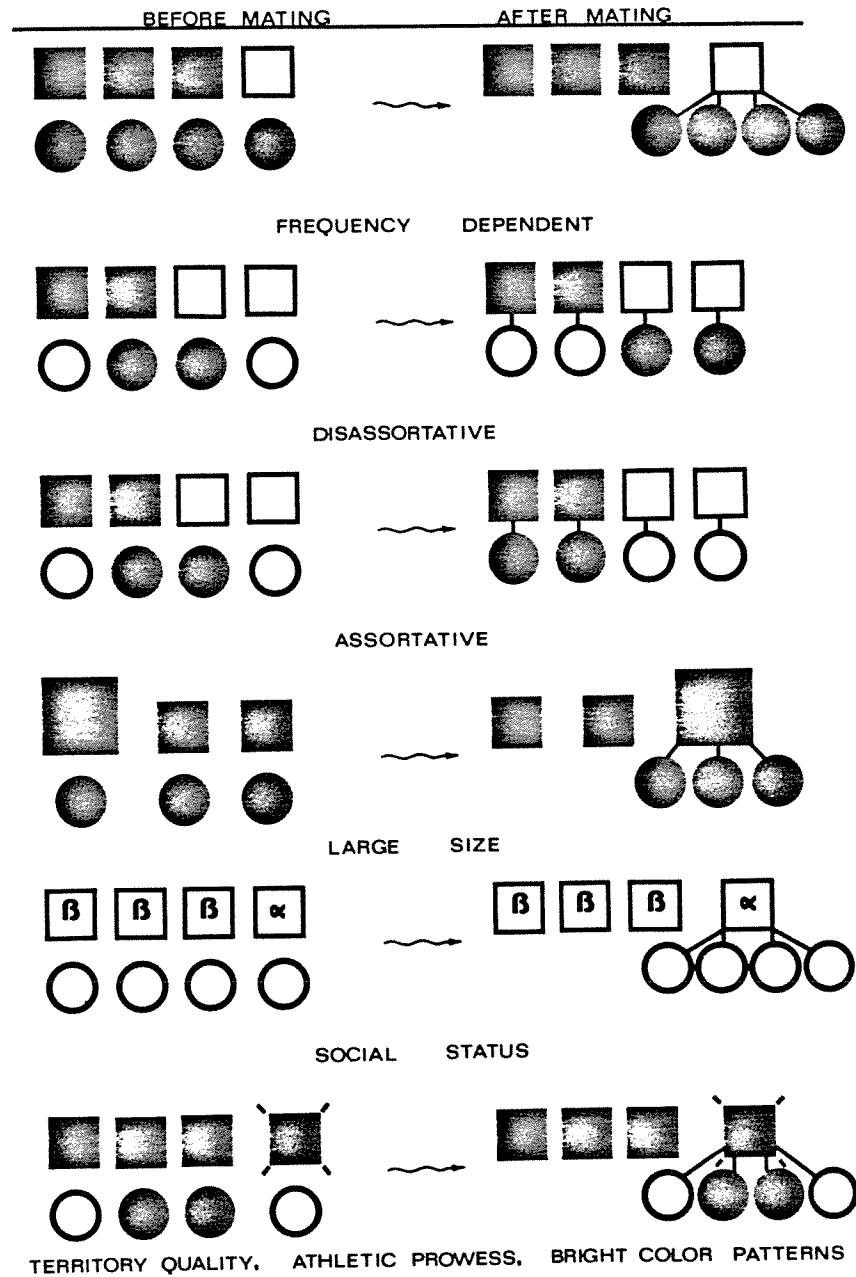


Fig. 1. A diagrammatic representation of some common types of mate choice.

For instance, breeding pairs in the marine snail Olivella biplicata are usually the same size (Edwards 1967). Yet, female preference or male intrasexual competition apparently do not play a major role in causing this assortative mating pattern. Large and small snails are active at different times of the day (nocturnal vs diurnal) and occupy separate intertidal areas (upper vs lower zones). Moreover, in those few instances when small males do make contact with large females, they are often mechanically incapable of copulating with them (Edwards 1967). A slightly different example is provided by Perrone's (1978) study of Cichlasoma maculicauda. In this species of fish, females tend to pair with males slightly larger than themselves. Perrone found that females preferred large males because: 1) they provide better nesting sites; and 2) while the pair guard their foraging young, large males can dominate smaller conspecifics at feeding sites. This means that if food is a limiting factor the young of a large male will grow more rapidly than those of a small one. Rapid larval growth allows each adult to mate more often and also shortens the period of time the young are susceptible to predation (Perrone 1978). Additionally, Perrone showed that males preferred large females as mates because they possessed more eggs than smaller ones. Thus, in this species both sexes prefer large mates, not similar-sized ones. Consequently, in breeding aggregations the larger males and females generally form pairs, leaving the next largest to pair and so on. Finally, Crow and Felsenstein (1968) suggest that assortative mating patterns may occur in animal species that commonly have subdivided populations (e.g., Pacific salmon). Members of such

populations usually share a common ancestry and thus are phenotypically similar to one another. So even if mating were random, the likelihood of phenotypic similarities between individuals comprising a pair would be high.

Mating Patterns in Spawning Populations of Pacific Salmon

Two papers (Painter 1962; Hanson and Smith 1967) have attempted to quantify the phenotypic relationships that may exist between fish forming pairs in Pacific salmon. Both investigations examined spawning populations of sockeye salmon (O. nerka) native to North American streams. The results of these studies were similar and revealed that the fish mated in an assortative fashion.

Painter's study took place on two small streams draining into Karluk Lake, Kodiak Island. He removed pairs by gaff hook and measured their body lengths. Correlation analyses performed on these data (stream one: $r=.540$, $r^2=.290$; stream two: $r=.424$, $r^2=.180$; $v=38$ in both cases) were significant ($\alpha=.05$) and indicated that males and females with similar body lengths generally paired with one another. However, not enough behavioral data were provided that could help explain how this mating pattern had occurred.

Hanson and Smith's investigation was more extensive. During two spawning seasons adult salmon trapped at the entrance of Four Mile Creek (Babine Lake, British Columbia) were marked with distinctive tags that reflected their length and sex. The fish were then released into the stream or placed into "pens" (fenced portions of the stream) where

observations were made to determine who paired with whom. The results of chi-square analyses showed that fish with similar lengths preferentially paired with one another. However, a lack of statistical independence might have invalidated some of their conclusions.

Reproductive Strategies of Male and Female Salmon

Before the origins of any mating pattern can be determined some of the basic biology of the animal has to be known. Pacific salmon have been studied extensively and it's recognized that they are generally anadromous, semelparous and lithophilic fishes. They have short (≤ 8 yr) but often complex life histories and are noted for their ability to migrate back to their natal streams to spawn. Fertilization is external with one or more males spawning simultaneously with a female. The females produce a few nutrient-rich eggs (often >1000 $\leq 10,000$) that are usually buried in two to seven gravel nests collectively referred to as a redd. Each embryo relies on the nutrients of its egg for several months, eventually emerging from the substrate as a fry, ready to continue the freshwater portion of its life cycle.

Detailed descriptions of spawning behavior have been presented by many investigators (e.g., Kuznetsov 1928; Schultz et al. 1935; Briggs 1953; Mathisen 1955; Hanson and Smith 1967; McCart 1970; Schroder 1973; Tautz and Groot 1975). These studies indicate that male and female salmon behave differently and that these differences are consistent throughout the genus. Figure 2 illustrates the basic reproductive pattern for each sex. After females reach maturity they have to

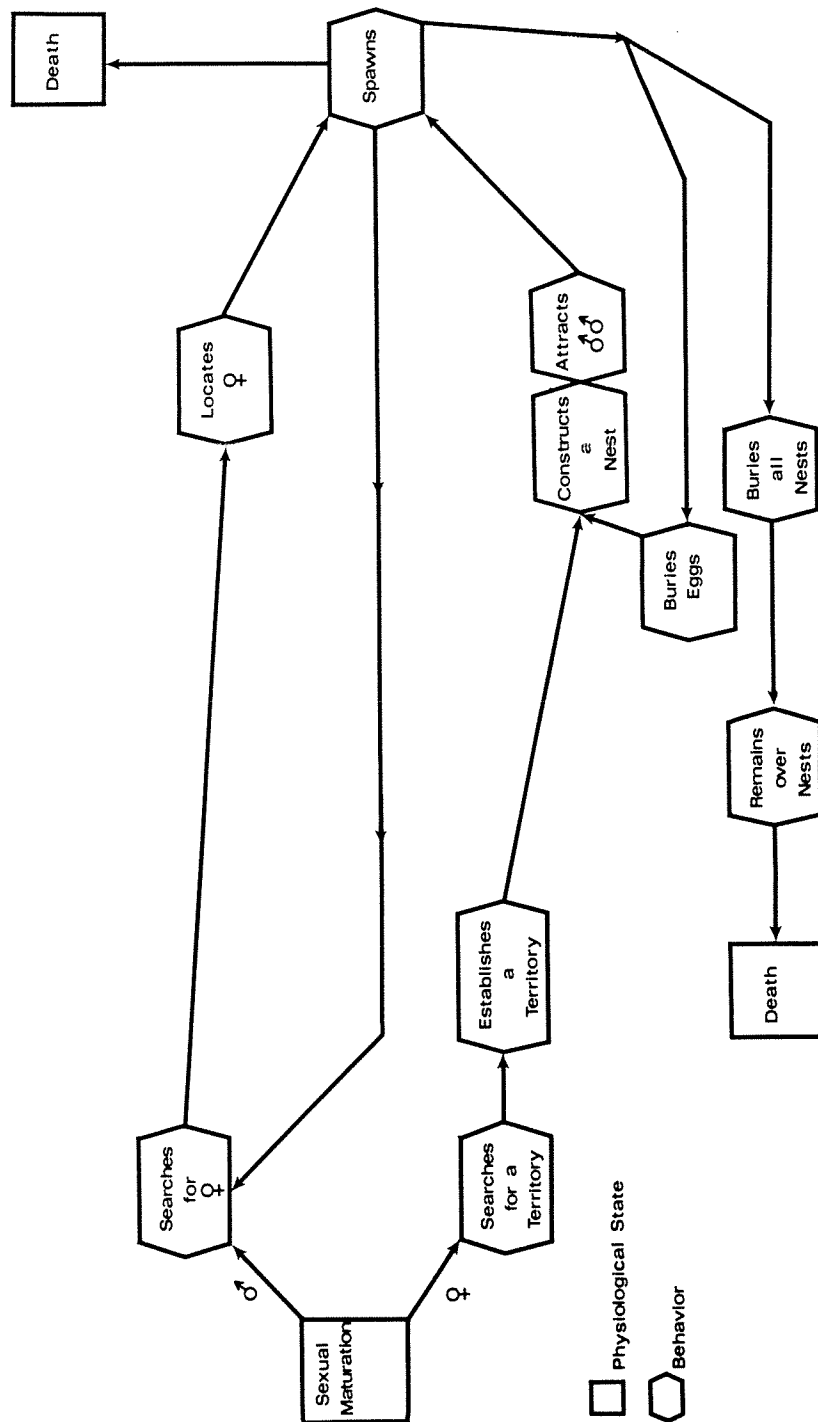


Fig. 2. A flow diagram illustrating the basic reproductive activities of male and female Pacific salmon.

complete three tasks to be reproductively successful. They must 1) locate an appropriate spawning territory and construct nests within its boundaries, 2) mate, and 3) defend their nest sites and buried eggs from dislodgement by competing females. Thus, except for an initial searching period females tend to remain over one area of a spawning ground until they die. Males on the other hand, are not bound to any portion of the stream bed and can move from one female to the next after egg fertilization has taken place.

Consequently, only under unusual conditons will salmon be monogamous. Polygamy occurs because 1) the sexual bond is promiscuous, 2) females do not become sexually active synchronously, but arrive on a spawning ground over a period of time, 3) sexually active females are a defendable resource, 4) males appear to be reproductively active for longer periods of time than females, 5) only females provide parental care, and 6) the young are basically self-sufficient. Under these conditions both types of sexual selection can play important roles in mate choice.

The flow diagram (Fig. 2) indicates that intrasexual selection may potentially occur in two areas: 1) among females while they seek out and defend their territories, and 2) among males while they search for females and defend them against potential sexual rivals. Epigamic selection is also expected since females invest heavily in their offspring and therefore, should be choosy about whom they mate with. Moreover, positive correlations between female size and egg number have been

observed in Oncorhynchus and thus males may prefer large females over smaller ones. Other types of male preference may also exist.

Some Unanswered Questions

The behavioral observations made by Hanson and Smith (1967) suggested that sexual selection was responsible for the overall assortative mating pattern they observed. However, I feel that both Painter's (1962) and Hanson and Smith's (1967) investigations left an array of basic questions unanswered. My 4-year study of spawning chum salmon and their subsequent progeny was an attempt to answer these questions, i.e.,

- 1) Will overall assortative mating patterns consistently manifest themselves in chum salmon demes as they apparently have in breeding populations in sockeye salmon?
- 2) How important is each component of sexual selection in mate choice and does their relative importance change under different conditions?
- 3) Do male and female chum salmon exhibit preferences for mates possessing certain physical or behavioral attributes?
- 4) If such preferences exist how do they potentially increase the inclusive fitness of an individual?
- 5) How has sexual selection influenced the reproductive strategies of male and female chum salmon?

In the next section I provide details on each of these general questions and describe the experiments used to answer them.

CHAPTER II. BACKGROUND INFORMATION AND EXPERIMENTAL DESIGN

Experimental Fish

The experimental animals were collected from Big Beef Creek, a typical Pacific Northwest stream that empties into the east shore of Hood Canal (Kitsap County, Washington State). Three runs of chum salmon migrate into the stream over a 5-month time period. The "early" run arrives in September and October and usually breeds in the lower 0.8 km of the stream (Koski 1975). The "middle" run enters Big Beef Creek in mid-November and December and most of the fish migrate upstream several kilometers or more (≤ 7) before spawning. The "late" run consists of a few (usually < 50) small and often silvery fish that reproduce in the lower reaches and upper intertidal areas of the stream in December and January. Data that would have differentiated fish originating from the middle and late runs were not recorded and thus these fish will be collectively referred to as the late run (after Koski 1975). Generally the fish are mature and spawning commences within several days (often hours) after their appearance in the stream (additional information about these fish and the Big Beef Creek watershed can be found in Cederholm [1972] and Koski [1975]).

Fish Trapping and Observation Facilities

As the fish migrated into Big Beef Creek they were captured in one of two traps located at the mouth of the stream and examined as previously described by Schroder (1973) and Koski (1975). Each fish was anesthetized with MS-222 (tricaine methane sulfonate), sexed, examined for

maturity, weighed on a spring balance (to the nearest 28 g), measured (tip of snout to fork in tail in millimeters), and aged by scale analysis using methods described by Koo (1962). They were then either released back into the stream, artificially spawned, or trucked 400 m or less and placed into an experimental stream (controlled-flow spawning channel) or a viewing chamber. The fish that were introduced into the experimental stream were tagged with large (3-cm dia) color-coded Petersen disks numbered from 00 to 99, so that individual fish could be identified and observed.

Experimental Stream

The experimental stream is located on a side branch of Big Beef Creek and is part of the University of Washington's Big Beef Creek Fish Research Station. It is 183-m long by 6.1-m wide and is subdivided by wooden walls into three parallel subchannels. Two of the subchannels ("A" and "B") are 1.52-m in width while the third ("C") is 3.0-m wide. Wooden pickets can be used to divide each subchannel into sections with varying lengths. During 1974 through 1976 I placed chum salmon into sections of subchannel "C" (3.05 m x 15.24 m) and observed mate selection under a variety of spawner densities and sex ratios. Each section had a .025% gradient (.25 m/100 m), a substrate of stream gravel (0.8 cm through 6.75 cm in dia) 75 cm in depth, and a black polyethylene wall that was 3 m in height. Viewing ports were cut at eye level along the length of the wall so that the fish could be observed without disturbing them. Water depth was usually 30 cm and velocity 22.5 cm/sec, but occasionally high tides reduced the water velocity to zero and increased the

depth to 1 m or more. These effects did not last for more than several hours nor did they appear to influence the fish. While the adults were in the spawning channel, surface water temperatures ranged from 13.9 to 2.2°C (1974: 13.9 to 5.6; 1975: 13.8 to 3.8; 1976: 11.7 to 2.2), and dissolved oxygen concentrations (as determined by a YSI Model 54 oxygen meter) were near saturation at all times. Further details concerning the construction, design, and additional uses of the experimental stream can be found in Beall (1972), Schroder (1973 and 1977), Koski (1975), and Duker (1977).

Viewing Chamber

In 1974, the upstream end of the experimental stream was developed into a viewing chamber so that observations on single pairs of chum salmon could be made. The chamber is composed of three parts, a concrete well (1.7 m x 3.3 m x 2.4 m) that is equipped with both horizontal (1 m x 1 m) and vertical (1 m x 1.5 m) windows, a 1.8-m x 3.3-m x 2.8-m storage house above the well, and a 3.05-m x 3.05-m gravel bed (Fig. 3). The bed is bordered on two sides by concrete walls and consists of a layer of stream gravel (1.2 to 6.2 cm in diameter) 20 cm thick, placed over a 20-mil polyvinylchloride liner. The up- and downstream ends of the bed can be blocked with wooden pickets and it is also possible to subdivide the bed into two 1.52-m x 3.05-m sections by a removable longitudinal picket.

To record the behavioral activities of single pairs or groups of fish placed into the chamber a videotape system was used. The component

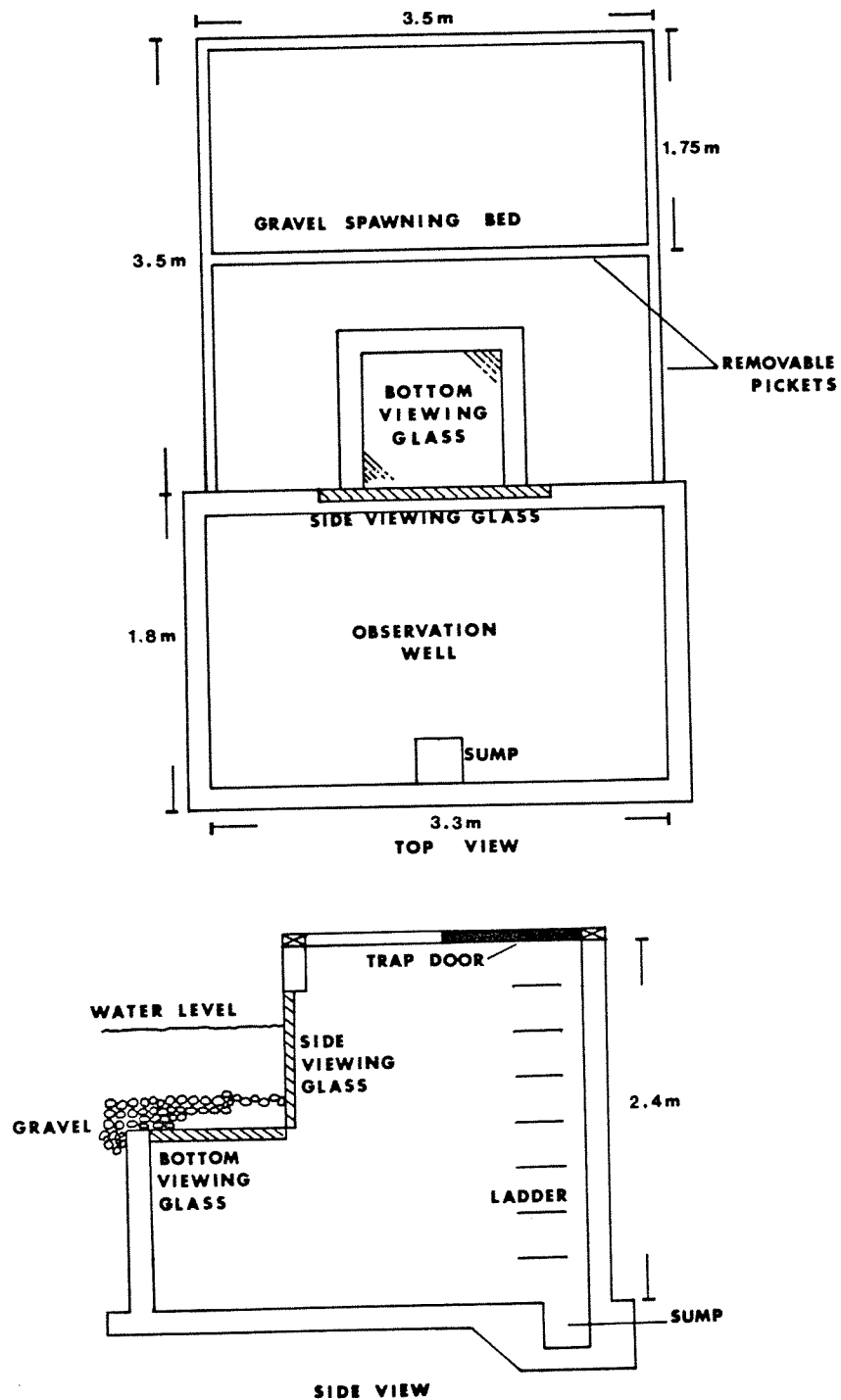


Fig. 3. Top and side views of the viewing chamber used to house the videotape equipment employed in producing behavioral records of spawning chum salmon.

parts of the system included a Sanyo Videotape Recorder, Panasonic "Nighthawk" camera, and a Setchell Carlson 10-inch video monitor. While operating in its slow-motion mode, the Sanyo VTR could record 7 continuous hours of observations per roll of videotape. The Panasonic camera had two interchangeable lenses, a f/1.8, 12.5-mm to 75-mm zoom and a f/1.5, 8.5-mm wide-angle lens. The camera also had a separate mesh silicon vidicon and could relay usable images when the background illumination did not fall below a 0.1 ft candle. With this equipment I was able to make continuous video recordings from early morning through dusk.

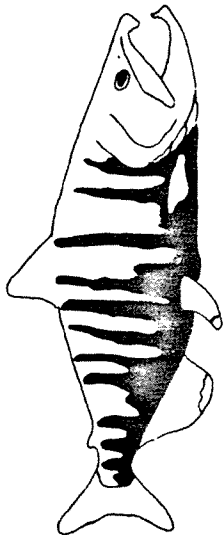
Field Observations in the Experimental Stream

All fish were placed into a section (3.05 m x 15.24 m) of the experimental stream within 24 hr of one another. Theoretically, this allowed each fish an equal opportunity to find territories, search for mates, and choose sexual partners. After being placed into a section the fish were observed periodically for several days or until the majority of the females had finished spawning. The fish were watched from dawn until dusk and each observation period lasted 20 to 60 min, depending on the number of fish and types of observations made.

The reproductive behavior of each individual placed into a section was recorded. Females were assigned to one of four states: 1) wandering (searches for a territory site), 2) active (prepares nests and spawns), 3) spent (through with egg deposition but still territorial), and 4) dispossessed (recently evicted from her territory by other

females). Males were likewise assigned to one of three states: 1) wandering (searches for females or lies quietly), 2) alpha (actively courts a female), and 3) satellite (lies in back of a pair and attempts to spawn with the female). Besides recording the reproductive behavior of each fish the color pattern of every male was also observed.

Chum salmon possess two distinct color patterns (Fig. 4). The bar color pattern consists of black and red streaks that run perpendicular to the length of the fish. From the posterior edge of the operculum to the tip of the pectoral fins the bars are black. From this point to the posterior edge of the pelvic fins (the widest part of the fish) the bars are a reddish-purple after which they become black once again. They overlie a mottled green-yellow background which becomes tan past the insertion of the anal fin. The stripe pattern consists of a single black-purple band that runs parallel to the length of the fish. Sometimes a fine white band borders the top and bottom of the stripe which tends to further enhance it. Measurements taken from videotape films showed that the stripe covers approximately 30% of the lateral surface area of the fish. Both sexes are able to quickly change (within seconds) from one pattern to the other, although females usually maintain the stripe pattern. The color patterns of males were observed to determine when shifts were made and whether these changes were associated with their reproductive status.



A. BAR COLOR PATTERN



B. STRIPE COLOR PATTERN

Fig. 4. The bar and stripe color patterns found on sexually mature chum salmon.

Determination of Overall Mating Patterns

To evaluate the effects of size on overall mating patterns in chum salmon demes I placed adult fish into 17 sections of the experimental stream and observed pair formation in conjunction with male body weight: female body weight. I preferred body weight to fish length because at the time of a fish's entrance into a section it gave a better indication of fish "size".

A pair was considered to be formed if a male courted a female (see Schroder 1973; Tautz and Groot 1975) throughout at least one observation period. Sometimes a male would "test" a female by quivering along her side, crossing back and forth over her back, or nudging her vent with his snout. If a female remained motionless or attacked the male, he usually left, but on some occasions a male might quietly remain by such a female for a period of time before swimming away. Male-female associations of this type were not included in the pairing data. If two males continuously fought over a female in a ritualized manner (see Chapter III, pp.113) both males were considered to be her sexual partners. Once one of them was defeated, however, only the dominant male was considered to be her mate. Any satellite males that were associated with a female were also excluded from the pairing data.

It was possible to determine the number of times that fish with similar or disparate body weights formed pairs since the identity of every fish in a section was known. Frequently, a male was seen courting the same female in subsequent observation periods. When this happened

the size ratio (i.e., male body weight:female body weight) of pair was recorded as many times as it was observed. These size ratios were transformed into quotients and placed into arbitrary classes, e.g., 0.5, 1.0, 1.5, etc., that reflected how much smaller or larger a male was than his female partner. The number of pairs falling into each class was compared against an expected value, i.e., one that would occur if the fish paired randomly with respect to size. (see Appendix I for an example of how these expected values were calculated.)

Statistical tests could not be used to determine whether the observed number of pairs (i.e., size-ratio quotients) falling into a particular class differed from the expected number. Siegel (1956, p. 41) states "...each observation [size-ratio quotient] must be independent of every other; thus one may not make several observations on the same [fish] and count each as independent. To do so produces an 'inflated N'..."

This lack of independence could be eliminated by using just one observation per fish or by only comparing the expected and observed values obtained from each observation period. But there are difficulties in both of these approaches. First, if only one observation is to be used per fish--which one should it be? Any choice is bound to be subjective because males and females commonly pair with many individuals. Second, the number of pairs observed during a typical observation period was often less than ten. Such a small sample size diminishes the power of any test. Moreover, since chi-square tests would be used, the

restrictions imposed by Cochran (1954, as cited by Siegel 1956) for small sample sizes would further reduce the amount of information such tests might convey. Therefore I made graphic comparisons between expected and observed values, and these analyses did provide information about overall mating patterns.

Examining the Affects of Sexual Selection on Males

Both intrasexual competition and epigamic selection may affect the number of eggs a male can fertilize. In this subsection I describe the experimental procedures used to: 1) Assess how size and physical condition may affect the ability of males to successfully compete for females under a variety of Operating Sex Ratios (i.e., under different intensities of intrasexual competition); 2) quantify the occurrence and success of satellite males, and 3) determine whether the size or color pattern of a male influences the behavior of the female he is courting.

What Operating Sex Ratios Represent and their Calculation. The association between male body weight and reproductive status was examined by observing the same 17 groups of fish used to determine overall mating patterns. I tried to vary the Operating Sex Ratio (OSR: the total number of sexually active males divided by the total number of gravid and territorial females) in every group by deliberately giving each one a different tertiary sex ratio (adult males:adult females). Every time an observation was made the number of sexually active fish was recorded. The amount of intrasexual competition that actually occurred within a group was estimated by calculating its OSR.

Sexually receptive females were relatively easy to identify since they prepared nests and spawned. The number of sexually active males in a section was more difficult to assess. After the fish were placed into a section of the experimental stream they invariably swam upstream until stopped by a wooden picket used to separate their section from an adjacent one. The fish would often push their beaks against this barrier for 12 hours or more before distributing themselves within a section. A male was identified as sexually active once he stopped pushing against the upstream picket and began to wander throughout his section. Moreover, I also assumed that once a male became sexually active he remained so until near death.

Examining the Relationship between Male Size and Reproductive Success. The males within a group were ranked according to their body weights and placed into one of three classes that represented their relative size. The heaviest or the top third were referred to as "large males," the middle third as "medium males" and the lightest or bottom third as "small males." Since the reproductive status of each male was recorded at every observation period, the percentage of time each individual spent as an alpha male could be estimated. This was accomplished by dividing the number of times a male was recorded as an alpha male by the total number of time he was observed. I used these percentages plus a one-way analysis of variance (ANOVA) to determine whether large, medium, or small males differed in their ability to court females under various OSRs. Each ANOVA had three treatments (male sizes) and the random variables were the percentages after they had been normalized by the

arcsine transformation (Zar 1974). To determine whether the variances were homoscedastic the F-Max Test (Sokal and Rohlf 1969) was used. After an ANOVA was performed, multiple comparisons using the Newman-Keuls multiple range test (Zar 1974) were made if the null hypothesis had been rejected.

Several males in a few sections were observed pushing their beaks against the upstream picket during the entire 2- to 3-day period their group was watched. These fish were excluded from the above data analyses. In other cases it was difficult to assess whether males were socially or physiologically inhibited from courting females. In these instances I have assumed that the males, regardless of their sizes, were sexually active at each observation period.

Observing the Association between Male Dominance and Physical Condition. Body size appears to be an accurate predictor of who "wins" agonistic encounters among males. But the physical condition of a male may also be important, since after a few days of freshwater residency the fish generally become weaker. The importance of this apparent loss in vigor was investigated by observing how many days a male could continue to dominate smaller opponents that had recently migrated into the stream.

Five males (hereafter referred to as "resident" males) were placed, one each, in five sections (1.52 m x 3.05 m) of the experimental stream. Every section had an "active" female plus a "challenger" (male) that was smaller than the resident male. The fish were watched as previously

described, with the reproductive status of each male being recorded at every observation period. At dusk both males were removed and the female was replaced by another one if she appeared to be "spent." The resident males were placed into a holding area while their challengers were returned to Big Beef Creek. At dawn every resident male was returned to a section along with a new challenger that had been captured the day before. At first the challengers were nine-tenths the size of the resident males. However, every time a resident male was "defeated" (i.e., lost his alpha male status), the size of the next male to challenge him was reduced by approximately 10%. This procedure was continued until all the resident males died.

I assumed that all males used in these experiments were sexually active and thus willing to compete against one another for females. Moreover, males that had defeated previous opponents were not assumed to be any more aggressive or tenacious than naive or recently dominated ones.

Measuring the Occurrence and Gametic Contribution of Satellite Males. When large differences exist among males in their ability to obtain mates alternative mating strategies may evolve among the "have nots" which circumvent the effects of intrasexual competition or female choice (Howard 1978). In breeding populations of salmon and trout, subdominant males have adopted the mating (behavioral) strategy of positioning themselves slightly downstream from a courting pair. These males continuously try to approach the female and spawn with her. Fish of

this type have been referred to as "satellite," "accessory," and "secondary" males. If there are more than two satellite males they usually lie in a semicircle (the open end facing the current) just downstream from the dominant or alpha male. Dominance hierarchies exist among satellite males with the strongest animals having the best access to the female (Kuznetsov 1928; Shapovalov and Taft 1954; Hanson and Smith 1967; McCart 1970; Schroder 1973).

The proportion of males using the satellite strategy in each section of the experimental stream was calculated by summing the number of satellite males recorded at every observation period and dividing this quantity by the number of sexually active males observed. Since each of the above groups of fish had a different OSR it was possible to determine when the satellite strategy first appeared and whether it increased proportionately with intrasexual competition.

A question that has long intrigued students of trout and salmon reproductive behavior (e.g., Jones and King 1952; Hanson and Smith 1967; McCart 1970) is whether satellite males fertilize any eggs during the spawning acts they participate in. I estimated the gametic contributions of alpha and satellite males during particular spawnings by using genetic variation analyzed by protein electrophoresis. This technique has also been used to examine paternity in a variety of other animal species (e.g., see Berry and Jakobson 1974; Tilley and Hausman 1976; Cobbs 1977; McCracken and Bradbury 1977; Nelson and Hedgecock 1977).

Since single gene differences can be used to determine paternity, I created situations where the alpha and satellite males that competed for a female had different allelic forms of the same protein. To do this the allozyme phenotypes (allelic forms of a protein) of the males were determined before spawning occurred. Electrophoretic examination of muscle, eye, and liver tissue obtained from chum salmon native to Big Beef Creek showed that the fish were polymorphic in five isozyme (enzyme) systems: 6-phosphogluconate dehydrogenase (6-PGDH), aspartate aminotransferase (AAT), phosphomannose isomerase (PMI), isocitrate dehydrogenase (IDH), and aspartate aminotransferase-3 (AAT-3) (Seeb, personal communication). Two of these isozyme systems (6-PGDH and AAT) have allozyme phenotypes that can be detected by examining muscle tissue. Consequently, genetic differences among males within these isozyme systems could be determined without killing the fish.

Sixty adult males were captured, anesthetized, and a small bit of muscle tissue (4 mm x 4 mm) was removed from the side of every fish. After being sampled, each male was tagged and released into a section of the experimental stream where he could easily be recaptured. The muscle samples were then electrophoretically analyzed by Mr. Jim Seeb, who used methods previously described by Utter et al. (1974), May (1975), and May et al. (1975). Once the allozyme phenotypes of each fish had been identified, I placed two or three males possessing different genotypes together with an active female and allowed them to spawn. The mating strategy employed by each male and his location at the time of spawning were

recorded so that the association between mating strategy and gametic contribution could be determined.

After the fish had spawned (with all males participating), the parental fish were killed and liver, eye, and also muscle tissue were collected and electrophoretically analyzed to identify all the allozyme phenotypes of each fish. Moreover, every egg deposited at each spawning was retrieved and incubated in a hatchery located next to the experimental stream. Six matings of this type were obtained and the zygotes collected from each spawning were kept in the hatchery until yolk absorption was completed. Because the males involved in every mating had different allozyme phenotypes (in one or two isozyme systems) it was possible to estimate the number of eggs each fertilized by examining muscle tissue samples obtained from the progeny. Consequently, 100 randomly chosen fry originating from each spawning were killed and electrophoretically examined.

The interpretation of the allozyme frequencies in the progeny depended on a number of assumptions. First, that the allozyme phenotypes used to determine paternity (in this case variant forms of AAT and PMI) represented genetic variation and were not environmental or ontological artifacts; second, that allozyme phenotypes rarely mutate into different forms; third, that genetic migration was controlled; fourth, that the allozyme markers used did not differentially affect egg-to-fry survival in any of their possible allelic combinations; fifth, that the

gametes bearing the genes responsible for each allozyme phenotype were equally viable; and finally that each male was fertile.

The genetic basis of the variant forms of AAT and PMI was established by controlled breeding experiments performed by Seeb and Wishard (1977). The neutrality of the genes responsible for each allozyme phenotype (at least from the gamete-to-fry stage) has not been formally tested, but the data presented by Seeb and Wishard (1977) clearly suggest that gametes and zygotes possessing different combinations of these genes survived equally well. Genetic migration (i.e., the intrusion of unwanted fish during a mating) was controlled by the experimental design, and because spontaneous mutation occurs so rarely (10^{-5} , Ihssen 1976), it was not considered an important source of error. I tested the fertility of some of the males that participated in these matings by artificially crossing them (using the "dry" method of fertilization) with the female they had previously spawned with. The eggs obtained from each cross were incubated in the hatchery until they had closed their blastopores. At this time a random sample of fifty eggs was collected from each cross and placed in Stockard's solution (85% distilled water, 6% glycerine, 5% formalin, and 4% glacial acetic acid). Since this solution clears the chorion it was possible to determine whether any of the eggs did not possess a developing embryo.

Determining the Effects of Male Size and Color Pattern on Female Choice. Previous studies on salmon mating behavior have not examined female choice in a quantitative manner, although empirical observations

made on female sockeye salmon suggest that they may discriminate among potential conspecific mates (Hanson and Smith 1967; McCart 1970). Theoretically, female salmon can influence who spawns with them in at least three ways. First, they may perform "incitation movements" that attract males; second, they may prolong nest construction; or third, they may attack certain males and attempt to chase them away. All of these tactics increase the vulnerability of males to attacks from other potential suitors and in the latter two cases may also cause a male to abandon a female and seek another partner.

To the human observer, male chum salmon differ from one another in two conspicuous ways--in their body sizes (both length and weight) and whether they possess the bar or stripe color pattern. To document how females responded to males possessing different color patterns or body weights, videotape films were made of 23 pairs that were deposited one at a time into the viewing chamber. Each female was provided with a male that was either one-half (type I pairs), approximately the same (type II pairs), or twice her weight (type III pairs). When a pair was filmed the gravel bed of the viewing chamber was subdivided by a longitudinal picket into two 1.75 m x 3.5 m sections. Since the contour of a spawning bed may influence female behavior (Pratt 1968; Tautz and Groot 1975; Schroder 1977; Duker 1977), the gravel bed was leveled by hand before each pair was filmed.

Eight hours prior to filming, the male and female were introduced into separate sections of the gravel bed, with the male always being

placed in the section that was adjacent to the observation windows. Just before the video equipment was turned on, the female was taken from her section and placed with the male. The fish were then allowed to spawn two or more time before they were removed from the viewing chamber.

When the videotapes were replayed I dictated the behavioral activities of both fish into a tape recorder. These observations were transcribed into a continuous ethogram that was divided into 1-min time intervals. The occurrence of 16 female and 10 male activities was quantified by summing the number of times each behavior was performed during every 1-min interval. The frequency of each behavior during nest construction was plotted to determine whether any type of female behavior "incited" or "attracted" her male partner.

Some of the videotapes were also analyzed to ascertain whether the nest digging behavior of a female changed because of the type of male that courted her. When a female digs she rotates onto her side and executes a set of rapid body flexures that raise and lower her caudal fin in a series of powerful strokes. To assess any changes in how a digging movement was performed the videotape was stopped just as the female started to rotate onto her side. The film was then advanced frame-by-frame and the number of body flexures needed to complete a dig was counted. This analysis was performed on three pairs (a type I, II, and III) while the females dug their second nests.

I also tested whether any male or female activities (e.g., agonistic interactions) occurred more or less often when pairs were composed of similar or dissimilar-sized individuals. Additionally, the amount of time it took each female to complete her first and second nest was measured along with the duration of each spawning act. Since nest construction consists of various types of digging movements and other behavioral activities (see Schroder 1973; Tautz and Groot 1975) it was necessary to artificially delineate when a nest began and ended. I arbitrarily decided that a female started her initial nest when she performed her first digging motion and completed it after she spawned. Subsequent nests were timed in a similar manner.

While recording the above data, I observed the color pattern of each male once every 7 min and found that the males persistently retained either the stripe or bar color pattern while the female prepared a nest. Consequently, I also used the videotapes to examine how females responded to males with different color patterns.

Female behavior may be affected by other variables besides the relative size or color pattern of her male partner. Biological factors such as her physiological condition and absolute body size, or environmental conditions such as water temperature, turbidity, light intensity, and the presence of observers in the viewing chamber, may also affect the frequency of various activities.

Prior to making any ethological comparisons among the filmed pairs the physiological condition of the fish was standardized. This was

accomplished by only using data acquired while the second nest was being prepared. The potential affect of absolute female weight on the amount of time required to complete second nests was examined by using correlation analyses. In these tests either the relative size of the male or his color pattern were held constant. How water temperature might influence spawning chum salmon is unknown; although Dodge and MacCrimmon (1971) showed that water temperatures below 2°C delayed and sometimes stopped female rainbow trout from spawning. Consequently, the association between water temperature and the amount of time needed to complete a second nest was examined by correlation. The color pattern or relative size of the male was also held constant in these analyses. Since the fish were filmed during daylight hours under conditions of low turbidity, I felt that these variables had a uniform effect on all the pairs. Finally, observers were occasionally in the viewing chamber (either to clean the window or adjust the video camera) but were rarely present while a pair prepared their second nest.

Measuring the Affects of Sexual Selection on Females

Depending on the amount of space available and the OSR within a spawning community, female chum salmon may compete among themselves for territory sites and possibly mates. In a previous study (Schroder 1973) I determined when female intrasexual competition for space occurred by varying the number of females placed into 20 (3.05 m x 15.24 m) sections of the experimental stream. When the area allotted each female was less than 2.7 m² (>17 females/section) some of the fish were socially inhibited from establishing a territory. However, the importance of size

and behavior in determining who could attract males or establish and protect a territory was not thoroughly examined.

Examining Competition for Space--the Importance of Size and Behavior.

Females from the same stock do not arrive on their spawning grounds simultaneously nor do they all become sexually active at the same time. Consequently, within any spawning community some females will be searching for territories while others will have already established them. The construction of nests, the burial of eggs, and their subsequent protection require energy and resources that cannot be obtained again. Because of these investments, territorial females should resist eviction. However, if space is limited and size is important in determining dominance among females, then large fish may prevent small ones from establishing territories, or usurp territories in order to spawn.

The relationship between female size and spawning success was examined in three sections of the experimental stream. The fecundity of every female placed into the sections was predicted by: 1) sacrificing females from the same stocks (late stock 1970 and 1971--also data from 1966-1970 was utilized to increase the sample size) used to fill each section; 2) weighing the sacrificed fish and counting the number of eggs each possessed; 3) performing Model II Regression analyses (body weight $\log_{10}$ vs egg number) on the above data; and, 4) using the subsequent regression equation to estimate the fecundity values. Koski (1975) gathered most of this information and also utilized it to predict the fecundity of chum salmon from Big Beef Creek, but he did not use Model

II Regression analyses (Sokal and Rohlf 1969). I decided to employ this method because both body weight and egg number measurements have inherent error terms that probably increase with the size of the fish.

The numbers of females placed in every section was sufficient (each was allotted less than 1.2 m^2) to ensure that intrasexual competition for space would occur. Observations were made to determine when each female established a territory, how long she held it, and the number of eggs she retained at the time of her death.

I divided the number of eggs a female retained by her estimated fecundity and used this value to determine her spawning success. These percentages were normalized by using the arcsine transformation, and correlation analyses were performed to determine whether a relationship existed between spawning success and absolute size when females competed for space.

The greater the area a female can defend and the longer she can protect it, the more secure her eggs will be from possible dislodgement and destruction from neighboring fish. Each territory contains all the nests a female constructs and any factor that influences the size of these structures might affect the total area each female will attempt to defend. The body size of a female could affect the amount of space needed to complete a nest because of the behavioral mechanism used to determine when the substrate is ready to receive eggs. This activity, called "probing," is the insertion of the anal fin and simultaneous lowering of the body into the heart of the nest. When the female tilts

her body at a 20-degree angle to make a probe the nest is usually complete (Tautz and Groot 1975). Consequently, the larger (longer) the female, the deeper the nest, and the bigger its surface area.

Besides the sizes of the nests their geometric arrangement and the spaces left among them may also influence overall territory size. Nests can be placed like beads on a string with the last nest furthest upstream or arranged in a diamond (Tautz, personal communication) or zig-zag pattern. In other cases a female may use the same nest site more than once thereby reducing the total area she needs to deposit her eggs (Schroder 1973).

Huxley (1934) showed that territory size in some species of birds resembled an elastic disc, expanding and contracting according to the amount of intrasexual competition for space. To see if territory size in female chum salmon responded in the same manner and to determine whether the size of a female affected the amount of space she could successfully hold, I measured territory sizes under three different spawner densities (6.6, 2.5, and $1.7 \text{ m}^2/\text{female}$).

Six (3.05 m x 15.24 m) sections of the experimental stream were used, and each section was provided with a grid system composed of 30-cm squares. The grid was placed over each section before any fish were introduced. It was made of tightly stretched nylon cord 2 mm in diameter and installed 20 cm above the water surface (Fig. 5). Every grid was divided by colored lines into five sections of 100 squares (or 110 points) each. The location of each female while she was constructing a

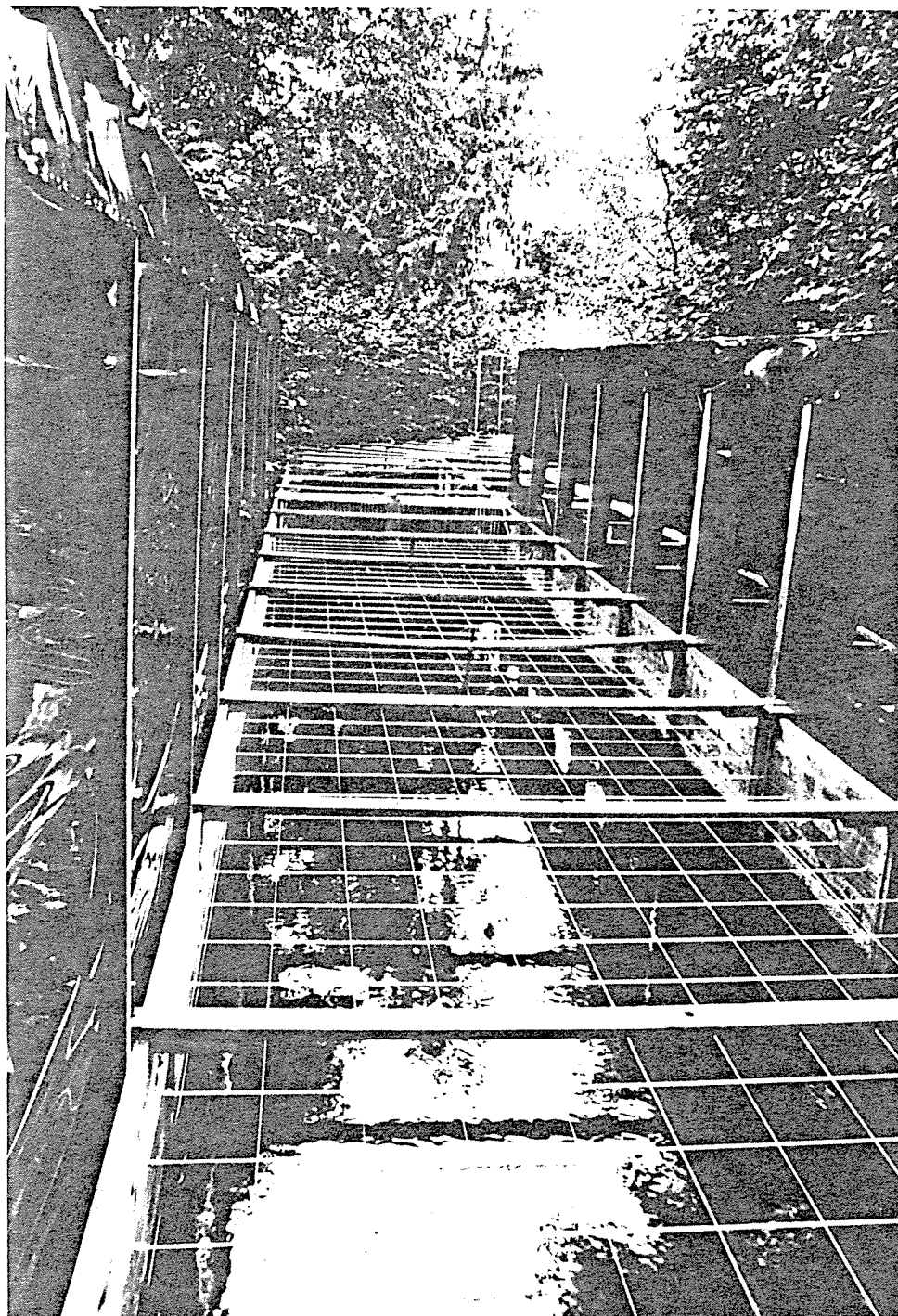


Fig. 5. The observation walls and grid system used in one section of the experimental stream to measure the territory sizes of female chum salmon.

nest was determined by using the grid. This information was plotted on maps and the area of each territory was calculated by the "cross section paper method" described by Welch (1948).

When this experiment was carried out no attempt was made to use females representing certain size classes but the total number of females released into each section was controlled. Thus the influence of female size and spawner density were examined by using a mixed model two-way ANOVA.

Determining How Size and Behavior Affect the "Attractiveness" of Female Chum Salmon. If the optimal reproductive strategy for a male chum salmon is to fertilize as many eggs as possible, then the "attractiveness" of a female should be based on the number of eggs she possesses (her absolute fecundity) or on her willingness to deposit them. A positive correlation between female size, either length or weight, and absolute fecundity has been found in almost every Pacific salmon population where this association has been examined (for chum salmon, see: Ivankov and Andreyev 1969; Bakkala 1970; Koski 1975). Consequently, female size may be an important criterion that males use when choosing their sexual partners.

Hanson and Smith (1967) observed that small female sockeye salmon consistently spent more time alone (i.e., were unattended by males) than large ones. Moreover, McCart (1970) while studying the same species found that satellite males, both sockeye and kokanee (the dwarf, fresh-water form of sockeye), were "...more likely to form associations with

female sockeye [i.e., large females] rather than associations, even dominant ones, with female kokanee [i.e., dwarf females]..." (McCart 1970, p. 89).

To determine whether male chum salmon would also prefer large mates, two females, one approximately twice as large as the other, were placed in a (3.05 m x 6.10 m) section of the experimental stream. When both females started to construct their first nests, a single male was introduced into the section. Continuous observations were made on all three fish until the male started to exclusively court one of the females. At this time, the fish were removed from the section and returned to Big Beef Creek. Additional fish were placed into the section in an identical manner until 19 repetitions of the experiment had been performed. How the fish interacted with one another and the number of times the male chose the largest female was recorded.

However, as Cox and LeBoeuf (1977) have suggested, what a female does may affect her "attractiveness" more than her absolute size. Some of the behavioral observations made on the groups of fish placed in the experimental stream to determine overall mating patterns were also used to test the following interconnected null hypotheses: 1) all females are equally "attractive" to males regardless of their reproductive behavior, i.e., whether they are "wandering," "active," or "spent;" and 2) the absolute size of a female plays no role in determining how "attractive" she will be to males.

To test these hypotheses the "attractiveness" of each female had to be quantified. This was done by summing the number of males (both alpha and satellite) attending her at each observation period and dividing this total by the number that potentially could have attended her.

By using this method it was also possible to estimate the "attractiveness" of each female while she was "wandering," "active," and "spent." All three of these "attractiveness values" were calculated for each female placed in the experimental stream. These values were normalized with the arcsine transformation (using Bartlett's correction factor whenever necessary, Zar 1974) and used as random variables in two statistical procedures. The first one was a mixed model two-way ANOVA without replication. The fixed treatment in these analyses was the reproductive status of the female (i.e., whether she was wandering, active, or spent) while the random treatment was her size. This test was employed to determine if the same female would attract more males at certain periods of her reproductive cycle than at others.

The second test, a one-way ANOVA, was used to ascertain whether size influenced the "attractiveness" of females. In these analyses the females in each section were ranked according to their body weights and then classified as a large, medium, or small fish. The heaviest third were referred to as large females and so on. Each class was used as a treatment group in the ANOVA and the random variable was the normalized "attractiveness value" of each female while she prepared her nests and spawned (i.e., when she was "active").

After the statistical tests were performed multiple comparisons were made with the Newman-Keuls multiple range test (Zar 1974) when the null hypotheses had been rejected.

Laboratory and Hatchery Experiments Used to Examine the
Question--Why be Selective?

Howard (1978) states that animals can assess the quality of their potential mates in two ways: 1) by the resources they possess, i.e., the location, size, and associated characteristics of their territories, and 2) by their phenotypic attributes, some of which may indicate overall vigor or to a certain extent their genetic quality. In some species, mate selection may be based on both of these criteria, while in others one criterion or the other may predominate (Howard 1978).

Any sexual preferences existing within a species for individuals holding certain resources or possessing particular phenotypes will be based on probable gains in genetic fitness (Fisher 1958). Therefore, to know why an animal discriminates among many potential mates it is necessary to assess the genetic advantages she or he will gain by being selective. Such gains can be indirectly measured by examining the number and quality of progeny produced from various types of matings (Fisher 1958).

Background Information on Temporal Changes in Fertility and Parental
Affects on Progeny Performance

One obvious factor that could influence the number of progeny a fish may produce would be the fertility of its sexual partners. It is doubtful that fertility per se is associated with age or size at maturity. However, since the physical condition of a spawning Pacific salmon

degenerates on an almost daily basis the viability of its gametes may decrease over time. If this is true, then males and females might prefer to mate with individuals that do not show signs of physical deterioration.

To determine whether males in poor physical condition could fertilize eggs, Mathisen (1955) captured a ripe, unspawned female sockeye salmon and divided her eggs into two portions. One portion was mixed with milt extracted from a "half-dead" male that was barely able to swim (a spent male) while the other egg lot was combined with sperm collected from two "vigorous" males. Each egg lot was incubated until pigmentation showed in the eyes of the embryos ("eyed stage"). The eggs in both lots survived equally well (1 to 1.7% mortality), indicating that at least some sockeye males remain fertile even though they are close to death.

Goryczko and Tomasik (1975) investigated whether temporal changes in sperm motility and egg viability occurred in brown trout (Salmo trutta). They collected milt from the same nine males at three different dates during one spawning season. Each time the males were stripped the resulting milt was mixed with eggs obtained from three females. The eggs were incubated until they reached the eyed stage and the percentage of nonfertilized eggs in every cross was recorded. The results of this study showed that the fertility of a male decreased over time and that eggs obtained from females late within a spawning season were less viable than those collected earlier.

Under some circumstances female salmon or trout may be socially inhibited from establishing a territory after they have arrived on a spawning ground (e.g., see Schroder 1973). However, some of these fish may eventually acquire a territory by migrating into less crowded areas or by reusing a recently abandoned redd site. Females that have been delayed from spawning, and in possibly poor physical condition could be less fertile than those who spawn soon after entering a spawning ground. Leitritz (1959) states that the fertility of a female trout (Salmo spp.) will decline as her eggs become overripe. Additionally, if such eggs are fertilized they are likely to produce more monstrosities or less viable and slower growing embryos than ripe eggs (Mrsic 1923, cited by Huxley 1923). Furthermore, the sex ratio of the young may also be influenced. Mrsic (1923, cited by Huxley, 1923) found that when he obtained eggs from a rainbow trout (S. gairdneri) 4 to 7 days after she had become ripe, the majority of her offspring were females. But if he did not collect eggs until 21 days after a female had reached maturity, then most of the resulting young ($\approx 67\%$) were males.

The above studies suggest that temporal decreases in male and female fertility probably occur in trout (Salmo spp.). However, whether such decreases were related to declines in physical condition or if they occur at all in Oncorhynchus remains uncertain.

Besides fertility or possibly the possession of overripe eggs, the size, age, and growth rate of a potential mate might also affect its

desirability. Hanson and Smith's (1967) and McCart's (1970) observations on the attractiveness of female sockeye salmon of various sizes indicated that males were aware of size differences in females. Furthermore, McCart (1970) observed that sockeye salmon females rarely attacked the large dominant males that courted them, but frequently chased male kokanee and sockeye jacks, often holding these small fish sideways in their jaws. Moreover, when he isolated female sockeye salmon with either "normal sized" sockeye, jacks, or kokanee males in pens, he found that the females would spawn with both sockeye males and jacks, but would not readily spawn with kokanee males. Burck (1965), while examining chinook salmon (O. tshawytscha) carcasses contributed further possible evidence of an awareness of size in female salmon. In the stomach of one of the females that was autopsied he found a small (95 mm long) precocious male. The female probably inadvertently swallowed the small fish while she was attempting to drive him off.

Both sexes may be "interested" in the size, age, or growth rates of their sexual partners for a variety of reasons. Two maternal effects, fecundity (the absolute number of eggs a female possesses) and egg size are often associated in a positive manner with both female size and age at maturity (Dahl 1918; Pritchard 1937; Rounsefell 1957; Allen 1958; Donaldson and Menasveta 1961; Privol'nev et al. 1964a, 1964b; Gray 1965; Smolei 1966; Bilton and Jenkinson 1966; Bilton 1970; Fowler 1972; Gall 1974; Hopley 1975; Koski 1975; Gall and Gross 1978; Kato 1978; Larsson and Pickova 1978; and many others). Both of these traits could affect the potential fitness of males. More fecund females might be expected

to deposit more eggs per spawning act. Those producing larger eggs may also be desirable as potential mates because egg size in salmonid fishes has been positively correlated with fry size (Dahl 1918; Gray 1928; Bilton 1970; McCart 1970; Fowler 1972; Gall 1974; Koski 1975; Hopley 1975) and in a few cases with post-emergent growth (Dahl 1918; Fowler 1972; Gall 1974).

Previous investigators have also linked progeny size, growth, and viability to maternal age. For instance, Koski (1975) collected and incubated chum salmon eggs with the same diameter but produced by two females that had matured at different ages. He found that the fry originating from the eggs produced by the older female (a 4-year-old fish) were larger at emergence than those arising from the younger (3-year-old) fish. Privol'nev et al. (1964a) did essentially the same thing with Atlantic salmon (Salmo salar) except that they also raised the young. After about 40 days of feeding they found that the progeny produced by their older female were growing slightly faster than those generated by the younger fish, even though the progeny were produced from similar sized eggs (identical wet weights). Ayles and Berst (1973) discovered that up to 31% of the variance associated with survival from hatching to yolk sac absorption in splake hybrids (Salvelinus fontinalis X S. namaycush) could be accounted for by the age of the female parent. Since biochemical studies on fish eggs have shown that lipids and other components vary with the age of the female (Nikolskii 1969, cited by Ayles and Berst 1973), they hypothesized that older females might produce qualitatively better eggs than younger ones.

Additionally, the growth rate of the female parent may affect how rapidly her offspring grow. Vladimirov (1973) feels that "...when the growth rate and fecundity of spawners increase there [will be] a simultaneous improvement in the quality of the sexual products and an increase in the viability of the progeny (Vladimirov 1973, p. 804). Savel'veva and Shuvatova (1972, cited by Vladimirov 1973) examined the progeny produced by female pike-perch (Lucioperca lucioperca) that had grown at different rates but were the same age (either 3, 4, or 5 years old). They found that the progeny produced from rapidly growing females grew faster and had better survival rates than those originating from slower-growing fish.

Similar observations on Atlantic salmon were made by Thorpe (1977). He divided the egg complement of his females into lots and fertilized each egg lot with sperm from a single male. When the subsequent progeny were reared, he found that a portion of the offspring in each family grew very rapidly. Consequently, as the fish were reared their lengths fell into a bimodal distribution. After performing correlation analyses between the length of the female parent and the percentage of her offspring that grew rapidly (i.e., were in the upper mode of the distribution), Thorpe (1977) concluded that faster-growing females produced greater percentages of fish in the upper mode than slower-growing ones, even though the females may have had identical life-history strategies.

Using the same species and a similar experimental design, Thorpe and Morgan (1978) partitioned the variance associated with progeny length,

smolting rate (i.e., the percentage of individuals in the upper mode that become smolts after 1 year), and mortality by male, female, family, and environmental effects. They found that 82 and 72% of the variation in progeny length (after 171-174 days of feeding) in the upper and lower modes respectively, could be attributed to the female parent, though only 1.7 (upper mode) and 10.7 (lower mode) could be accounted for by the male parent. Both parents influenced the smolting rate of their offspring and how well they survived. In another study, Thorpe and Morgan (in press) discovered that the progeny fathered by Atlantic salmon parr developed "...faster to the smolt stage than those [produced by] male salmon maturing at a later stage."

Paternal effects on progeny characteristics have also been examined in other salmonid fishes. Childs and Law (1972) measured and weighed embryo coho salmon (O. kisutch) just before they hatched and concluded that those fathered by jacks (2-year-old males) utilized their yolk materials more efficiently and developed faster than embryos generated by normal males (3-year-old fish). Coho salmon were also used by Clarke et al. (1977) when they evaluated embryo size 63 days (≈ 600 T.U. °C) after fertilization. In this case, the eggs fertilized by underyearling male coho salmon had bigger embryos than those that had been fertilized by older and larger males.

The influence of paternal size and age at maturity on how rapidly young sockeye salmon grew was examined by Bilton (1970) and McCart (1970). Neither investigator could detect any male effect on how

rapidly the fish in their experimental populations grew. Hopley (1975), utilizing chinook salmon, made a variety of artificial crosses based on parental age at maturity. He, on the other hand, found that 4-year-old males produced larger smolts than either 3- or 2-year-old male parents at the end of his rearing experiment.

To determine whether young Atlantic salmon fathered by parr grew differently than those produced by older and larger males, Jones and King (1950) conducted two rearing experiments that compared the growth rate of half sibs. They found no difference (based on mean lengths) in how rapidly their half-sib populations grew. However, Thorpe and Morgan (in press) point out Jones and King (1950) did not realize that the lengths of the fish in their reared populations were bimodally distributed. Even if this difficulty did not exist, their results are hard to interpret because information on the life-history strategies of the large males they used is not mentioned. If these animals had matured as parr, then each progeny lot would have been fertilized by males possessing identical, not disparate life-history strategies (for a discussion on this point, see Thorpe and Morgan, in press).

Both paternal and maternal size in Pacific salmon may reflect how large their offspring will become at maturity. Ricker et al. (1978) noticed that the average size of adult pink salmon (O. gorbuscha) native to British Columbian and some Alaskan streams has steadily declined since 1951. After an extensive review of meteorological data and trends in gear use by the commercial fishery, they concluded that the selective

removal of large fish by troll and gillnet fisheries was responsible for the downward trend in fish size. Since pink salmon invariably mature at age 2, the observed decrease in body size was attributed to a decline in growth rates--i.e., slower growing parents in these stocks apparently produce slower growing offspring. This apparent linkage between parental size and offspring growth rate may, if widespread, have a profound impact on mate choice preferences within the genus Oncorhynchus.

Evidence recently synthesized by Frey (personal communication) and first presented by Donaldson and Menasveta (1961), Ellis and Noble (1961), Donaldson and Bonham (1970) and Reimers (1978, and unpublished MS) suggests that parental genotypes in chinook salmon (and by inference other Pacific salmon) may also strongly influence when their offspring will mature. For example, Reimers (1978) reports that in 1968 a hatchery was established on the Elk River (Oregon State) and a breeding program was begun using chinook salmon native to the stream. Slightly less than 50% of all the adult fish in the river were 2-year-old males (jacks) but none of these fish was used in the hatchery breeding program. By 1974, the number of jacks returning to the hatchery had been greatly reduced, although a similar reduction had not occurred in the wild population.

Consequently, in 1974, parental crosses based on age at maturity (3-year-old ♀♀ x 3-year-old ♂♂ and 5-year-old ♀♀ x 5-year-old ♂♂) were made at the hatchery, and fry from each cross were differentially marked and released. When these fish returned to the hatchery, it was found

that a large number of jacks had been produced by the 3 x 3 crosses, while very few had been generated by the 5 x 5 matings. These data suggest that early-maturing parents tend to produce more early-maturing offspring than older ones (Frey, personal communication).

Similar types of crosses with different parental ages were performed by Ellis and Noble (1961) on chinook salmon returning to the Deschutes River (Washington State). These investigators crossed 2- (jacks) and 3-year-old males with 3-year-old females. They found that 30% of the male offspring produced by 2-year-old males returned as jacks, while only 12% did if the male parent had been 3-years-old. Moreover, male age did not appear to influence when their daughters matured, for 88 (2 x 3) and 89 (3 x 3)% of the resulting females matured at age 3, although none matured at age 2 (Frey, personal communication).

After reviewing this evidence, Frey (personal communication) hypothesized that the genetic mechanism controlling age at maturity or its expression might be sex-specific. To test this hypothesis, Frey tabulated the results of a series of artificial crosses made by Donaldson and his co-workers. These investigators utilized chinook salmon returning to the University of Washington hatchery and made the following crosses: (female age before male) 3 x 2, 4 x 2, 3 x 3, and 4 x 4. The progeny produced from these crosses again indicated that older parents generally create older offspring. Furthermore, there was a proclivity for sons to reach maturity at the same age as their fathers and for daughters to follow the life-history strategy of their mothers

(Frey, personal communication). The importance of these propensities on mate choice in chum salmon will be discussed later on.

Objectives of the Hatchery and Laboratory Studies

The hatchery and laboratory experiments described below examined the relationship between parental phenotypes and progeny abundance and quality. Specifically, I attempted to answer the following questions. Does the phenotype (mainly the physical state of deterioration, size or age at maturity) of an individual potentially provide information to other fish about: 1) its fertility, absolute fecundity and egg size, 2) its age at maturity, 3) how rapidly and efficiently its progeny utilize yolk materials, 4) the rate at which its young develop, 5) the occurrence of monstrosities and mortalities in its young during the incubation phase, 6) the size of its young at emergence, i.e., when their endogenous food supply is almost exhausted, and 7) the early growth and survival of its progeny after they start to feed on exogenous food?

Determining Whether Temporal Changes in Fertility³ Occur in Spawning Chum Salmon

In lieu of what was known about temporal changes in salmon (*Oncorhynchus*) fertility, it became important to determine whether fertility decreased over time and if so whether salmon preferred mates that did not show signs of physical deterioration.

³Fertility in these experiments was defined as the ability of an individual to produce gametes capable of uniting with either an ova or sperm to produce a zygote. No examinations were made to determine whether the number of nonviable zygotes or monstrosities produced by an individual changed as it aged in freshwater.

Measuring Male Fertility. To determine whether temporal changes in male fertility occurred, three males that migrated into Big Beef Creek were placed in a 1.5-m x 3.05-m section of the experimental stream. Milt was extracted once a day from each male until he died. Just before the milt samples were collected, approximately 300 eggs were stripped from a female that had recently entered the stream (a different female was used each day of the experiment). The eggs were weighed on a Mettler P2010 balance to the nearest .1 g and divided by weight into three equal lots. Each lot of approximately 100 eggs was then mixed with 3 ml of milt obtained from one of the males.

To mimic natural spawning the eggs and milt were kept separate until they were simultaneously poured into a glass beaker filled with 200 ml of freshwater. After the gametes were introduced into the beaker it was gently swirled for 60 sec. The resulting egg lots were incubated separately in Heath Tecna trays that had been divided into six compartments by strips of Plexiglass. Black plastic covered each incubator and every tray was supplied with 18.9 L (5 gpm) of 9.6 (C) artesian water.

Each artificial cross (egg lot) was allowed to accumulate approximately 60 temperature units (°C) before it was preserved in Stockard's solution. The number of viable eggs was then determined by examining the gross appearance of each egg. An egg was considered fertilized if the marginal periblast, germ ring, or embryonic shield was visible (photographic plates of these structures can be found in Mahon and Hoar 1956, and Bakkala 1970).

Previous observations made on five Big Beef Creek chum salmon males (Schroder 1975) had shown that the water content (i.e., evaporable constituents) in their milt tended to increase as the fish remained in freshwater. This trend led to the speculation that such a dilution in milt solids would be negatively correlated with fertility. Samples of the milt collected from the three males used to examine temporal changes in male fertility were utilized to test this hypothesis.

Every time the males were artificially stripped, the milt that was not used in the fertilization experiment was poured into a previously weighed aluminum foil pan. The pan plus the milt was weighed on a Mettler P163 balance to the nearest 0.01 g. Each pan was then placed in a Precision Thelco Model 17 drying oven and dried for 24 hr at 97°C. After drying, the milt samples were put into a vacuum dessicator containing anhydrous calcium chloride and allowed to cool before they were reweighed on the Mettler balance. Water content was calculated by weight difference and these values were compared to the number of eggs that had been fertilized with milt from the same sample.

Measuring Female Fertility. Similar methods were used to examine temporal changes in female fertility. Three females were placed in a small section (1.5 m x 3.05 m) of the experimental stream. Approximately 100 eggs were collected from each female once every 24 hr until she died. The egg samples collected on any given day were fertilized by the same male, but milt was collected from a different male each day the experiment lasted.

The eggs and milt were mixed, incubated, preserved, and visually inspected for zygotes as previously described. Moreover, the water content of the milt used throughout the experiment was determined, so that the fertility of each male could be estimated.

Assessing Whether Fecundity and Egg Size Are Correlated with Body Size

If a great amount of the variation associated with fecundity and egg size can be explained by body size, then it might "pay" males (in a genetic sense) to prefer large mates. Correlation analysis (in particular r^2 or the coefficient of determination) can be used to describe the amount of variability in one random variable (such as egg size) that can be accounted for by correlating that variable with a second, normally distributed random variable--e.g., body weight (Zar 1974). From 1974 through 1976, I examined the association between female size (both length and weight) and fecundity, and also egg size (diameter, wet and dry weight) in 461 chum salmon that had migrated into Big Beef Creek. One hundred and sixty-four of the females originated from the early run (107 in 1975, 57 in 1976), while an additional 297 (197 in 1974, 100 in 1975) were late-run fish.

Every female was anesthetized in MS-222, and length, weight, and age (determined through scale analysis) data were obtained on each fish. The caudal peduncle was then severed and the fish were bled thoroughly before any eggs were removed. In 1974, the egg complement of each female, including her ovarian fluid, was stripped (through incision) into a dry, preweighed polyethylene bag. The bag and its contents were

then weighed to the nearest 10 g on a Chatillon 6 K x 10 g balance. After the total egg complement was weighed, a sample of 60 to 200 eggs (plus ovarian fluid) was withdrawn and weighed on a Mettler P1200 balance to the nearest 0.01 g. These two weights, plus the number of eggs in the sample were used in the following algebraic formula to estimate the fecundity of each female:

$$\text{Fecundity of female } Y = \frac{(\text{No. of eggs in her egg sample})(\text{Total egg wt.} - \text{plastic sack wt.})}{(\text{Wt. of her egg sample})}$$

In 1975 and 1976, the eggs were stripped into a plastic colander and consequently any ovarian fluid that did not coat the eggs was removed before they were initially weighed. A Mettler P2010 balance was used in 1975 and 1976 to weigh the total egg mass produced by each female to the nearest 0.1 g.

After the 60 to 200 eggs that were removed from the egg complement of each female were weighed, they were placed in separate glass jars partially filled with freshwater and allowed to water harden for 12 hr in a refrigerator. The eggs were then hand-counted and three subsamples of 20 eggs (chosen at random) were removed from each jar. To determine the diameter of the eggs in each subsample, the eggs were placed on a measuring board held at a 25° angle. Once the eggs were in place, the measuring board was lightly tapped three times and the total length of the eggs (to the nearest .5 mm) was recorded. After being measured the eggs were blotted dry on paper towelling, placed in a preweighed aluminum foil pan, and weighed to the nearest 0.01 g on a Mettler P163

balance. Each subsample was next dried in an oven at 97°C for 24 hr, allowed to cool in a dessicator and then reweighed on the Mettler balance.

The above data were utilized to estimate the amount of information a male could possibly obtain about the egg size and fecundity of potential mates based on their body size. Statistical analyses were performed to determine: 1) whether an increase in body size was accompanied by increases in egg size and fecundity, and to calculate the amount of variation in these traits that could be attributed to body size, and 2) whether older females possessed more or larger eggs than younger ones.

Examining Whether Body Size Reflects the Growth Rate and Age of Mature Chum Salmon

Previous studies on salmon and other species of fish have implied that both parental age and growth rate may affect various progeny characteristics (see pp. 54-58). Clearly, for a fish to preferentially mate with individuals possessing "desirable" age or growth characteristics, it has to be able to detect differences in these traits among possible sexual partners. In mature chum salmon such differences could be reflected by their body sizes. For example, if substantial differences in size occur among fish with dissimilar ages, then discrimination based on age becomes possible. If such differences are not evident, then the age of a potential mate is a cryptic trait and choice based on that characteristic is unlikely to evolve.

The growth rate of a chum salmon might also be discerned by its size if the fish within a deme are the same age. Presumably in this case the largest animals would be the fastest growing ones within the population. Such aggregations of fish could occur in two ways. First, by a genetic mechanism (e.g., dominance or lack of variation) that locks all the fish returning to a spawning area into the same life history strategy. And second, by a propensity for fish originating from different brood years to return to the same stream at different times during a spawning season.

Field evidence gathered on a few chum salmon runs has indicated that there may be seasonal trends in the arrival times of fish produced from different brood years. For instance, Mattson and Rowland (1963) found that fish returning to Traitors River (S.E. Alaska) in August 1962, were primarily 4 years old, but as the run continued into September over half of the fish migrating into the stream were 5 years old. Helle (1979) observed a similar type of segregation in Olson Creek (Prince William Sound, Alaska) except that in this stream older individuals tended to arrive sooner than younger ones.

Since data on the arrival time, age, and size of almost all the chum salmon that spawn in Big Beef Creek were routinely gathered, I used this information to test the following null hypotheses: 1) size differences do not exist among fish that mature at different ages, and 2) fish originating from different brood years migrate and spawn in Big Beef

Creek at the same time. To test the first null hypothesis I used one-way ANOVA or "t" tests to compare the lengths and weights of fish (within a sex) that had matured at different ages but returned to the stream during the same run and year. The second hypothesis was tested by examining when males and females of different ages arrived into Big Beef Creek.

The Artificial Crosses Used to Investigate Parental Effects on Progeny Performance

Even if differences in body size allow salmon to recognize older or faster growing⁴ individuals, such information will be of little use unless such differences can be associated with progeny performance or abundance. To decipher any such connections three artificial crosses were made.

The relationship between male size at maturity and progeny growth was examined in the first (Cross I) artificial cross. Nine males and nine females collected from the late run in 1974 were used to create three replicates of a 3 x 3 factorial cross. The females were all the

⁴When age is held constant, size at maturity may reflect the relative growth rates of fish within a stock, but only if these fish experience similar environmental conditions (e.g., availability of food, sea temperatures, etc.). In some of the analyses presented in Chapter III and described below I have assumed that fish returning to Big Beef Creek at similar times, with the same age and sex, lived in equivalent rearing environments. For instance, if two 4-year-old females returned to this stream at approximately the same time (both year and date) I assumed that the larger of the two had a greater intrinsic growth rate.

same age (4 years old) and approximately the same weight (4.03 to 4.42 kg) but the males were either 3- or 4-years-old and their body sizes fell into three distinct classes, "small" (2.21 to 3.06 kg), "medium" (4.71 to 4.96 kg), and "large" (6.83 to 8.19 kg). Each factorial cross was created by spawning three males (a small, medium, and large fish) with three females.

Prior to fertilization the egg complement of each female was split into three aliquots (equal parts) and each aliquot was then mixed with semen collected from one of the males. Three half-sib families were thus obtained from every female and each family was fathered by a male with a different body size. Moreover, every male also produced three half-sib families, but in this case each family had a different female parent. By repeating this process three times, nine replicates of three types of crosses (medium ♀ x small ♂, medium ♀ x medium ♂, and medium ♀ x large ♂) based on male size at maturity were created.

A second artificial cross (Cross II) examined the effects of paternal age and egg size on utilization of yolk materials by embryos. Eight females (all 3-year-olds) and five males (one 2-, two 3-, and two 4-year-olds) obtained from the early run in 1975 were used to produce 24 families. The egg complement of each female was again split into thirds and each third was fertilized by a male that had reached maturity at a different age. Hence, eight replicates of three types of crosses (3 ♀ x 2 ♂, 3 ♀ x 3 ♂, 3 ♀ x 4 ♂) based on paternal age were produced.

A third artificial cross (Cross III) examined the effects of two parental ages on progeny growth rates. Sixteen females (eight 3-year-olds and eight 4-year-olds) and 24 males (twelve 3-year-olds and twelve 4-year-olds) selected from the late run in 1975, were crossed with one another to create 32 families. The egg complement of every female was split into two aliquots and each aliquot was fertilized by a male that had matured at a different age. This procedure produced eight replicates of the following four types of crosses: 3 ♀ x 3 ♂, 3 ♀ x 4 ♂, 4 ♀ x 3 ♂, and 4 ♀ x 4 ♂.

Most of the males (16) fertilized one aliquot of eggs, however, eight males (four 3-year-olds and four 4-year-olds) were used to fertilize two aliquots. In these cases each aliquot of eggs originated from a female that had matured at a different age. Thus, two half-sib families were produced from each of these fish and like those created from every female, they represented a different union of parental ages. By incubating and rearing these families it was possible to test if different combinations of parental age brought about consistent differences in progeny performance (i.e., embryonic and post-emergent survival and growth).

The Procedures Used to Fertilize and Incubate the Families Obtained from Crosses I, II, and III. The "dry" method of artificial fertilization was used to make Crosses I, II, and III. The fish were weighed, measured, aged, and tagged with Petersen discs (to guarantee proper identification) before they were spawned. Each male was wiped free of

water and mucus, and artificially stripped into buckets (one to three-- depending on the Cross) lined with dry polyethylene bags.

Every female was anesthetized, bled, stripped of her eggs by incision, and had her fecundity and egg size estimated as previously described (cf., pp. 63-65 Chapter II). To reduce contamination and prevent egg activation before fertilization each female was wiped clean of water, mucus, and blood just prior to egg removal. After the total egg mass of each female was weighed it was divided into the necessary number of aliquots (through weight) by using either a Chatillon (Cross I, 1974) or Mettler P2010 (Crosses II and III, 1975) balance. Each aliquot was then gently poured into the polyethylene bag that contained semen originating from the desired male parent.

Immediately after the gametes were mixed (within 1 hr) they were taken to an incubation facility. The families resulting from Cross I were incubated and reared in a barn about 3 km away from the station that had a 225 μ m supply of (8.7 to 8.9°C) artesian water. The hatchery used to incubate the families produced from Crosses II and III was located next to the experimental stream about .5 km away from the egg collection site, and it also had an artesian ($\approx$ 300 μ m, 9.0 to 9.9°C) water source. Vertical-stack fish incubators produced by the Heath Tecna Corp. were employed in both hatcheries, and since the head box, plastic plumbing, etc., used in the barn was installed in the newer Big Beef Creek facility both hatcheries were very similar.

Once the gametes had arrived at a hatchery, water was added to each polyethylene bag to activate the eggs and wash away any impurities and excess semen. Every family was then placed into its own incubator tray. The location of these trays within the 16-tray incubator stacks was randomized to eliminate any effects caused by tray position.

Six environmental conditions, light, dissolved oxygen (DO), water temperature and velocity, density--i.e., the number of individuals/cm², and incubation substrate are known to affect how salmonid embryos and alevins survive and perform during incubation. Consequently, these variables were controlled to make the incubation environment experienced by each family equivalent to one another.

Many studies have shown that chronic exposure to light during incubation may cause less efficient usage of yolk materials, losses in weight before hatching, acceleration or delay in development, increases in mortality, visual impairments, and decreased alertness in salmon and trout (Smith 1916; Bell and Hoar 1950; Disler 1953; Eisler 1957; Brannon 1965; Poon 1977). Thus, all the incubator stacks were covered with opaque polyethylene so that the eggs and alevins would not be exposed to light except when they were periodically examined.

Since the water used in each hatchery originated from an artesian spring, temperature remained essentially constant ($\pm .4^{\circ}\text{C}$ as determined by twice daily thermometer readings) throughout an incubation period. However, the amount of dissolved oxygen in the water was relatively low (≈ 4 to 5 ppm). Therefore, it was aerated by feeding it through a

perforated pipe (7.5 cm in dia) that ran the length of a 6-m long x 1-m wide x 1-m deep fiberglass "head box." Moreover, after the water exited the pipe it was splashed over a stainless steel screen. This technique raised the dissolved oxygen concentration to 9 to 10 ppm ($\geq$ 80% saturation).

The head box, which was situated directly above the Heath incubators supplied every stack of trays with 18.9 ℓ pm (5 gpm) of water. Hence, the average apparent velocity in each tray was 883 cm/hr, well within the recommended range of 54 to 5400 cm/hr (higher or lower velocities may affect survival and decrease size at emergence--Brannon 1965; McNeil and Bailey 1975; Poon 1977). The flow rate into each stack was routinely measured in ml/10 sec by using a stopwatch and a graduated cylinder.

Egg and alevin densities in salmon incubation systems are also known to influence progeny performance. For instance, Poon (1977) incubated chum salmon eggs in Heath trays and gravel boxes (single layer of crushed gravel) at three different densities (0.94-.96, 1.88-1.92, and 3.75-3.85 eggs/cm²) under three flow regimes (25, 75, and 225 cm/hr). He found that eggs incubated in the gravel boxes at the lower density had the lowest mortality rate regardless of water flow. A similar but less pronounced result (4.88% vs 5.94%) also occurred in the Heath trays. During my experiments only 1/2 to 1/3 of the eggs produced from a female ($\approx$.52 to 1.25 eggs/cm²) were incubated within a tray. Therefore, I feel that any possible density effect on survival was avoided.

Just prior to hatching the eggs were "shocked" and any unfertilized or aborted ones were removed. Each family was then transferred into a Heath tray equipped with an Astroturf mat. The (1283 cm²) mats were attached to the bottom screen of the trays by using a Dennison Buttoneer and either plastic or Neoprene buttons. After the eggs hatched, the alevins inserted themselves among the plastic blades and remained quiescent throughout the incubation period.

Examining Progeny Performance During the Incubation Period. Four general categories of progeny performance were examined, survival, rate of development, yolk material efficiency, and size at emergence.

Measuring pre-emergent survival. Pre-emergent survival in salmonid fishes has been linked by various investigators to egg size (e.g., Frost and Brown 1967, as cited by Ayles and Berst 1973; Fowler 1972; Hopley 1975) and as mentioned earlier with parental age (Ayles and Berst 1973; Gall 1974) and possibly growth or size.

To determine whether fertility and progeny survival in chum salmon were affected by parental age, body size, or egg size, I monitored the occurrence of unfertilized eggs, pre-emergent death, and monstrosities in the families produced by Cross III. Every dead egg that was removed from a family was placed in Stockard's solution to determine whether it possessed a zygote. These data were used to compute the percentage of eggs in each family that had not been fertilized (determined by dividing the number of unfertilized eggs by the total number of eggs present in a family) and to calculate embryo (pre-hatching) mortality by dividing the

number of fertilized but aborted eggs by the total number of fertilized eggs in a family. Alevin (post-hatching) mortality was ascertained in a similar manner but in this case the number of hatched but aborted alevins was divided by the total number of alevins produced by a family. The percentage of live fry in each family that were malformed either because of mechanical shock (e.g., twins, swollen yolks, spine curvatures, etc.) or genetic causes (e.g., albinos, mosaics, calcareous eruptions, fin abnormalities, etc.) was also determined.

The above percentages (four/family) were transformed (with the arcsine transformation) and two statistical procedures were used to judge whether the aforementioned parental traits affected fertility and progeny survival. First, correlation analyses were performed to determine if associations existed between three parental traits (i.e., length, weight, and egg size) and fertility, embryo and alevin mortality, and the frequency of monstrosities. And second, model I two-way ANOVAs were utilized to assess whether male or female age or certain combinations of parental age influenced fertility and progeny survival.

Examining how quickly the young produced by various families developed. The length of time it takes a salmon zygote to develop into a fry may also have subtle effects on its ultimate survival. If it uses all of its yolk materials too rapidly or too slowly, it may find that stream and estuarine conditions are not ideal, e.g., food supplies may not be abundant enough to allow it to obtain maximum growth, or heavy concentrations of predators may have been drawn into an area because of

previous concentrations of fry or their own migration patterns. Based on these considerations it seemed reasonable to determine if any parental traits (including egg size) influenced how quickly yolk material could be converted into body tissues.

I measured differences in "developmental rate" in two ways. First, by determining if alevins originating from various families (produced by the same Cross) absorbed yolk materials at different velocities and second, by assessing whether fish from different families had the same developmental condition factor⁵ (Bams 1970) after the incubation period was terminated. In the latter case only families that had accumulated an identical number of temperature units were compared.

Undoubtedly water temperature is the most important factor influencing how quickly a salmonid zygote utilizes its yolk and develops into a fry (Velsen 1980). However, paternal age (Childs and Law 1972; Clarke et al. 1976) and other parental traits may also affect how rapidly a zygote grows. Because the families created by Crosses I, II, and III were either all created on the same day or were incubated in water with a constant temperature, it was possible to test (without the confounding

⁵Bams (1970) formulated the following developmental condition factor (K_D) which can be used to estimate the proportion of yolk material remaining in salmon alevins by measuring their lengths and weights:

$$K_D = \frac{\sqrt{10^3 \text{ wet weight in mg}}}{\text{length in mm}}$$

The values obtained from this formula are independent of fish size and they decrease in a linear fashion as the animal utilizes its yolk and begins to starve (Bams 1970).

effect of water temperature) whether certain parental traits influenced how fast chum salmon zygotes utilized yolk materials and developed into fry.

Four sets of half-sib families produced by Cross III were used to examine the importance of egg size and paternal age on how rapidly alevins utilize yolk material. Twelve alevins were removed from each family on six separate occasions during the incubation period. After they were collected the alevins were placed in 10% formalin for 24 hr to coagulate their yolks. Each yolk was then separated from its larval tissue by dissection, placed in groups of three into aluminum foil pans, dried at 97°C for 24 hr and weighed to the nearest .01 g on a Mettler balance. In this manner four dry yolk weights were obtained on every family at each sampling period.

Model I regression methods (Sokal and Rohlf 1969) were used to determine how quickly fry from these families used their yolk materials. The independent variable in these analyses was the number of temperature units (°C) that the alevins had acquired by each sampling period, and the dependent variable was the dry weight of three yolks.

After the regression analyses were completed, an analysis of covariance was used to ascertain whether the alevins in one or more of the families utilized their yolk materials at different rates. Because this proved to be the case a Newman-Keuls multiple range test was employed to test differences among the eight slopes. As mentioned earlier (cf., pp. 69), each set of half-sib families came from the same female but

were fathered by males that had matured at different ages, therefore it was possible to examine the effects of male age on the rate of yolk use. Moreover, because each of the four females had different egg sizes the influence of this variable could also be examined.

Immediately after an incubation period was terminated, samples of fry from every family created by the artificial crosses were removed so that their developmental condition factors (Bams' K_D) could be calculated. Three groups of 100 fry from each family created by Cross I were blotted dry on a damp sponge, placed in a tared beaker filled with water, and weighed to the nearest .01 g on a Mettler balance. Fork lengths (TSFT) of 30 to 40 fish representing each family were also obtained by anesthetizing and measuring portions of the previously weighed fry. The mean wet weight and fork length of the sampled fry were then determined and used to calculate an overall K_D for each family. In Crosses II and III, 25 fry were randomly selected from every family, killed with a heavy dosage of MS-222, and individually weighed and measured. Consequently, instead of an average K_D value (as in Cross I) each of these families was represented by 25 values.

The above developmental condition factors were used as random variables in several statistical tests. First, a model III (i.e., a mixed-model) two-way ANOVA without replication was used to determine whether paternal size influenced the average K_D value of alevins originating from families created by Cross I. The fixed treatment in this analysis was male size, i.e., small, medium, or large (cf., p. 69), while the

random treatment was the egg source or female. Second, similar analyses, except with replication, were used to investigate the effect of male age on the developmental condition factors of alevins derived from the families generated by Crosses II and III. And third, correlation analyses were performed on some of these data to discover whether the developmental condition factor of a fry at the end of its incubation period was influenced by the estimated dry weight of the egg it originated from.

Determining how economically fry from different families utilized their yolk materials. The size of a chum salmon fry at emergence is another trait that is closely connected to its potential survival. Predation on these small fish is intensive and appears to be size-selective, e.g., Levanidov (1954), Kanid'ev (1966), Beall (1972), and Sato (1972) all showed that small chum salmon fry were more vulnerable to predation than large ones. This size bias probably occurs because large salmonid fry can swim faster than small ones (Bainbridge 1958; Bams 1967) and also their size makes it difficult for many predators to swallow them (Beall 1972; Walker 1974). Moreover, Houston (1961) found that large chum salmon fry (≈ 60 mm) adapted to seawater more rapidly than small ones (≤ 50 mm). He also observed that the locomotor performance of salmonids is depressed while the animals adjust to salt water and therefore speculated that smaller, "less efficient" fry would be susceptible to predation for longer periods of time than "more efficient," large fry.

Furthermore, Koski (1975), working with chum salmon, and Bagenal (1969), with brown trout, demonstrated that large unfed fry survived longer without food than small ones. The ability to resist starvation could be an important trait because unpredictable environmental factors can delay emergence (Koski 1975) and possibly affect the exogenous food supplies the young rely on.

One factor that can affect fry size at emergence is how efficiently the zygote has utilized the energy reserves of its egg. Yolk materials passing into a developing salmon are used to form new cells or support already existing tissue (Gray 1928). However, the proportion of yolk diverted into these tasks changes over time because the respiratory and katabolic costs of maintaining an embryo increase as it becomes more complex (Gray 1928). Consequently, the absolute amount of yolk material that is used to maintain an embryo steadily increases as the animal develops.

Because of the above considerations, it is clear that less-developed embryos will have better "cumulative efficiencies" (because such individuals have put less of their yolk into maintenance and more into body tissues) than those that are nearer to emergence. Thus, to make meaningful comparisons among fry based on how economically they have utilized their yolk materials it is imperative that the fish be in the same stage of development, i.e., have similar K_D values. Consequently, when I determined whether alevins originating from different families varied in their ability to convert yolk materials into body tissue, the

statistical comparisons were restricted to those families (created by the same Cross) that had fry with equivalent developmental condition factors.

I estimated how efficacious the alevins had been in converting their yolk resources into body tissues by using the following procedures. At the conclusion of each incubation period (890, 895, and 880 temperature units °C for Crosses I, II, and III, respectively) a random sample of fry (nine individuals from Cross I, 25 from Crosses II and III) was removed from every family. The sampled fish were killed (cf., p. 77) and then divided into either three (Cross I) or five (Crosses II and III) equal subsamples. Each subsample was placed into an aluminum pan, dried for 48 hr at 97°C, and after cooling in a desiccator weighed to the nearest .01 g on a Mettler balance. The total dry weight of every subsample was then divided by the number of alevins in each pan. This value which represented the mean dry weight of the alevins was in turn divided by the estimated dry weight of the eggs they originated from. The resulting quotients were estimates of the overall percentage of yolk material that the alevins had converted into body tissue. These values were normalized by the arcsine transformation and used in a variety of statistical tests.

The influence of sire size and age on utilization of yolk material was examined in two ways. First, model III two-way ANOVAs were used to determine the importance of these traits on fry produced by Crosses I and II. The fixed treatment in these analyses was either male size

(Cross I) or age (Cross II), while the random treatment was once again the egg source or female. Second, a "paired-sample t-test" (Zar 1974) was employed to determine the importance of male age in the Cross III families. In this analysis the "mean efficiency" of alevins originating from the same female but fathered by males that had matured at 3 or 4 years of age were compared. Moreover, a correlation analysis was performed on data acquired from the Cross I families to determine whether dry egg weight covaried with yolk material utilization.

Examining the influence of parental traits on progeny size.

The size of a chum salmon fry at emergence has also been linked with egg size (both diameter and weight) and maternal age at maturity (cf., pp. 53 - 54 , Chapter II). However, before describing the experiments used to examine the influence of these and other parental traits on progeny size, the physiological factors that can bias any size comparisons among fry produced by different families will be briefly mentioned. When a salmonid alevin utilizes its yolk materials it absorbs water and increases both its body length and total wet weight. But since body tissues possess 2.5 to 3 times as much water as yolk material, the total dry weight of an alevin decreases as it grows (Gray 1928; Bams 1970; Poon 1977). Therefore, when making size (dry and wet weight or length) comparisons among alevins produced by different parents the fish should have the same proportion of yolk and embryo tissue--i.e., be in the same developmental stage (Brannon 1965; Bams 1970; Poon 1977). Otherwise the influence of yolk material on body weight (wet or dry) or length is not considered, and "detected inequalities" in these values may merely reflect that the

fish are in different stages of development. Thus, before size comparisons among fry produced by different families were performed I determined through ANOVA and multiple comparison tests which groups (families) of fry had similar K_D s and hence could be compared with one another.

I based all of my size comparisons on body weight (both wet and dry) because I felt that it was a more sensitive index of fry size than either length or volume. In the preceding subsection I mentioned that a random sample of fry was removed from each family at the completion of its incubation period. The dry and wet weights of these individuals were used in the tests described below.

The importance of dry egg weight and the paternal traits of body weight and age-at-maturity on fry size at emergence were examined simultaneously by using Model III two-way ANOVA techniques. Again, the fixed treatment in these analyses was either male size (Cross I) or age (Crosses II and III), while the random treatment was dry egg weight. To further explore the association between dry egg weight and alevin weight (at the conclusion of an incubation period) correlation analyses between these two random variables were performed.

Furthermore, a Model I two-way ANOVA was employed to determine whether female age at maturity influenced the size of her offspring at the completion of an incubation period. In this analysis (which used data acquired from four Cross III families) size comparisons were made among fry originating from eggs with the same dry weights (fixed

treatment "a") but produced by females that had matured as either 3- or 4-year-old fish (fixed treatment "b").

How the Families Created from Crosses I and III were Reared. The few studies which have investigated the early marine survival of chum salmon concluded that most of the natural (as opposed to fishing) estuarine and ocean mortality occurs within 40 to 100 days after they enter salt water (Ricker 1964; Parker 1968). Predation may be the major cause of this mortality (Parker 1971; Sibert 1972; Cooney et al. 1978; Cardwell and Fresh, unpubl. MS), although disease and starvation may also decimate chum salmon populations. Since predation on these fish is often size-selective (cf., p. 78), parental fish that produce initially large or rapidly growing fry should have a selective advantage over those that do not. Consequently, if the phenotype of a mature fish can be used to predict the growth rate or initial size of its potential offspring, then this information could be employed by adult salmon while they choose their sexual partners. Crosses I and III were made primarily to determine whether parental phenotypes conveyed this kind of biological information.

The families produced by Cross I were reared for 49 days in wooden troughs supplied with artesian water. The 30.5-cm wide x 30.5-cm deep x 240-cm long troughs were divided by wooden-framed nylon mesh (1.6 mm Delta) screens into three 30.5-cm x 30.5-cm x 78.5-cm rearing areas. To account for possible location effects the three half-sib families produced by each male were placed into all three possible rearing areas

(head, middle, and tail) in three different troughs, whereas the three half-sib families originating from each female were always reared in the same trough.

During the 7-week rearing period water depth in each trough was maintained at 16.5 cm. Water temperature was a relatively constant 8.8°C (Range of 8.7 to 8.9, $n = 98$) and flow averaged 9.5 lpm (S.D. 2.42, $n = 63$) but varied somewhat from trough to trough. Flow rates were determined by collecting the outflow water of each trough in an 18.9 l bucket for 30 sec, measuring the amount collected in a graduated cylinder, and multiplying this value by two. Like flow rates, dissolved oxygen concentrations in each trough were determined on a weekly basis. a Hach kit or model 54 YSI oxygen meter was used to sample the outlet water of each trough. These values did not vary much from one trough to another and were reasonably high (9.5 ppm, S.D. 0.23, $n = 9$) at the beginning of the rearing period but gradually declined to ≈ 7.9 ppm (S.D. 0.36, $n = 9$) at the conclusion of the experiment.

The fry were initially fed a dry starter mash for several days and then were switched to an Oregon Moist Pellet diet (OMP) (Hublou 1963). Each family was fed in excess of 14 to 16 times a day (0800 to 1700 hr). As the fish grew the diameter of their food was changed so that it equaled approximately 1/40th of their length. Uneaten food and feces were siphoned out of each rearing area once every day to prevent the water from fouling.

To evaluate fish growth 25 individuals were removed from each family once every 7 days. The fish were captured by dip net, placed into 18.9 l plastic buckets half-filled with water, and transported to the freshwater laboratory located at Big Beef Creek. To help ensure that the wet weights of the fish would be equivalent to their live weights, every bucket was supplied with an air stone so that the fish would have sufficient oxygen (Parker 1965). Moreover, to reduce the influence that undigested food pellets might have on both wet and dry weights, the fish were always collected in the morning before their first scheduled feeding period.

The order in which the samples were processed was not totally random because I weighed and measured the samples that originated from the same female, i.e., those representing maternal half-sib families, one right after the other. However, the groups of samples representing different females were not processed in any particular sequence. After the fish in a sample had been killed by a heavy dosage of MS-222, individual lengths (TSFT to the nearest .5 mm) were taken, and the animals were layed on moist paper toweling. Just before the fish were weighed they were blotted three times on each side on dry paper toweling. The above procedures were implemented to reduce absorption of water after death and to remove moisture adhering to the outside surface of the fish in a standardized manner (Parker 1965).

Once a fish had been blotted dry it was placed into a pre-weighed aluminum foil pan that rested on a Mettler P163 balance. Five fish were

placed one at a time into each pan. Their individual weights were ascertained by subtracting the weight of the pan plus any fish that may have been in it, from the weight recorded after the fish was added. Because the fish were weighed in the same order that they had been measured, the length and weight of every individual was determined. The five pans of fish from each sample were next put into an oven, dried for 48 hr at 97°C, allowed to cool in a desiccator and reweighed on the Mettler balance to the nearest .01 of a g.

The Cross III families were sampled in the same way but were reared in a slightly different manner. In this case each family was fed for 98 days (14 wk) in its own 30.5-cm wide x 45.7-cm deep x 112.2-cm long wooden trough. The troughs were placed outside the hatchery located at Big Beef Creek and were protected from snow, rain, and direct sunlight by a roof made of green fiberglass. The 32 troughs used in this rearing experiment were split into two equal groups and placed back-to-back so that one group faced away, and the other faced toward the hatchery building. A "header box" equipped with an overflow standpipe rested on the backs of the troughs and supplied each one with its own water supply. Because the position of a trough may influence how the fish within it grow and survive, a random number table was used to assign each family a rearing location.

Water height was again controlled and it averaged 18.8 cm (S.D. 0.79, range 17.2 to 20.6 cm, $n = 32$). Thus, each family was provided with approximately $.065 \text{ m}^3$ of rearing space (S.D. 0.003, range .058 to

.070 m³, n = 32) as opposed to .040 m³ of space for the Cross I families. Since the rearing water originated from an artesian well, temperature remained fairly constant ($\bar{x}$ = 9.59, S.D. 0.16, n = 832) but it did vary somewhat according to climatic conditions (range = 9.2 - 10.0°C). Flow rates into each trough were determined three times a week by capturing inflowing water in a container for 10 sec and measuring the amount collected in a graduated cylinder. The flow rate into every rearing area could be regulated, so the flow rates into every trough were kept fairly similar ($\bar{x}$ = 6.9 lpm, S.D. 0.16, range 5.6 to 8.0, n = 832) during the entire rearing period. Dissolved oxygen concentrations were determined as before but tended to be lower ($\bar{x}$ = 6.73 ppm, S.D. 0.53, n = 64) than those experienced by the Cross I families, although they remained relatively constant through time (range = 7.4 to 5.8 ppm).

The dry starter mash fed to the families produced by Cross I caused abrasions on the gills and other body surfaces that later became sites of Saprolegnia infestation. To prevent this from occurring to the fry produced by Cross III they were reared entirely on an OMP diet. Moreover, unlike the families created by Cross I that were fed approximately 4% of their wet weight/day, these families received a little over 16% of their wet weight in food/day (or $\approx$ 1% of their body weight per feeding). As in the first rearing experiment the troughs were cleaned once a day with a siphon.

While the Cross III families were being reared every effort was made to ensure that the environmental conditions within each trough were

as similar as possible to one another. Besides regulating flow rates, I also adjusted the rearing density (i.e., grams of fish/liter/min) within each trough on a weekly basis. By following this procedure all the families had the same density or grams of fish/liter/min at the beginning of each rearing week.

After the rearing experiment was terminated I used one-way ANOVAs to determine whether the troughs had similar water temperatures and concentrations of dissolved oxygen. The results of these tests (water temperature $F = 0.65$, $< F .05 (2) 7, 824 \approx 2.29$; dissolved oxygen $F = 0.13$, $< F .05 (2) 7, 56 \approx 2.53$) indicated that the troughs were apparently similar with respect to these variables.

One other factor that could potentially affect the observed growth rate of a family was also investigated. If males grow more rapidly than females (or vice-versa) and if some families possessed more males than females, then observed inequalities in growth rates among the families may merely reflect a difference in sex ratios rather than other types of genetic differences. I examined this possibility by weighing, measuring (cf., p.) and sexing (using methods described by Jensen and Hyde 1971) 800 individuals originating from 20 families (40 fry were examined per family) after the rearing experiment was completed. A "paired t-test" was used on some of the resulting data to compare the mean wet weight of male and female siblings. The results of this test ($t = 3.245$, $> t .05 (2) 19 = 2.093$) showed that the males in each family tended to be heavier than their sisters after 14 wk of rearing.

Consequently, it was important to determine whether the sex ratios present in these families were similar to one another. To determine this I performed a 2 x 20 chi square analysis (Siegel 1956) and found no differences ($\chi^2 = 19.30 < \chi^2 .05, 19 = 30.14$). Therefore, I assumed that the sex ratios in all of the families were equivalent and that the apparent difference in male and female growth rates did not bias the statistical procedures used to compare the growth rates of one family against any of the others.

Examining Progeny Performance During the Rearing Experiments. The performance of each family was evaluated by determining how rapidly its members grew and, in the case of the families created by Cross III, by how well they survived. Growth was estimated by using Model I regression techniques (Sokal and Rohlf 1969). The independent variable (i.e., x) in each analysis (one per family) was time in weeks, and for every rearing week there were five replicates of the dependent variable (y). Each y represented the mean dry weight of five fry after this variable had been transformed by using the Log_{10} transformation. Since the slope of each regression line expressed the change in y (mean dry weight) that occurred on the average with a unit change in x (i.e., per week) I used this value to estimate the growth rate of a family.

Once the slopes had been calculated, analyses of covariance were employed to determine if any differences occurred among them. If dissimilarities were evident, then a Newman-Keuls multiple range test was used to ascertain which slopes differed. Because the families produced by Crosses I and III were reared under slightly different conditions, the

kinds of comparison that could be made among their families were not the same.

For example, when the families produced by Cross I were raised no effort was made to standardize the environment within each rearing area. Consequently, it was only possible to compare the growth rates (i.e., slopes) of maternal half-sib families because they had been reared in the same trough (although in different portions of it) under similar rearing densities (i.e., grams of fry/liter/min).

Since the families originating from Cross III were raised under more controlled conditions the types of comparisons that could be made were much more extensive. As in the analyses performed on the families produced by Cross I, growth comparisons were made between the maternal half-sib families. Moreover, it was also possible to: 1) compare growth rates between paternal half-sib families, 2) perform an analysis of covariance on pooled regression data to determine if certain combinations of parental ages produced more rapidly growing fry, 3) test with correlation analyses some of Vladimirov's (1973) hypotheses (cf., pp. 55) about the importance of parental growth (as reflected by size) on the growth of their young, and 4) examine with correlation analyses the influence of dry egg weight on growth and progeny size at the end of the rearing experiment.

Data collected on the families created by Cross III were also used to determine whether egg size, parental size, or age at maturity influenced progeny viability once exogenous feeding began. Records of the

number of fish dying (of natural causes) per week were kept on each family. These values were divided by the number of fish present in a family at the beginning of each rearing week and therefore every quotient equaled the percentage of fish within a family that died during a particular week. From the above data I calculated an average mortality rate/week (to facilitate statistical analyses) on every family. This was done by transforming the weekly mortality percentages with the arcsine transformation, summing them, and dividing the total by the number of weeks the fish were reared (i.e., by 14).

Correlation analyses between dry egg weight or parental size (both length and weight) and the average weekly mortality rates experienced by the families were performed to determine: 1) whether fry originating from large eggs suffered a higher mortality rate than those produced by small eggs (e.g., Fowler 1972; Hopley 1975) or 2) if individuals created by large maternal or paternal fish survived better than those begot by smaller parents (e.g., Vladimirov 1973). Two basic types of correlations were performed, those where parental age was held constant and those that used data gathered on all 32 families.

The effect of certain combinations of parental ages on progeny survival was examined by using a Model I two-way ANOVA. In this analysis male and female age were the fixed treatments while the average weekly mortality rate of families representing each type of parental cross (i.e., 3 x 3, 3 x 4, 4 x 3, 4 x 4) were the random variables.

Summary of the Overall Objectives of the Experimental Design

Briefly, the emphasis of the hatchery and laboratory studies was to determine whether the physical appearance (as opposed to the behavioral phenotype) of an adult chum salmon conveys any potential information about the abundance and "quality" of the offspring it may produce. The field observations, on the other hand, attempted to extract some of the information an individual's behavioral phenotype might broadcast about its desirability as a potential mate, and to gather empirical observations on who spawned with whom under a variety of social circumstances. In Chapter III I use the results of these studies to answer the questions posed in the introduction and to speculate on the adaptive significance of the reproductive strategies employed by each sex.

CHAPTER III. RESULTS AND DISCUSSION

Factors Influencing the Creation of Overall Mating Patterns in Chum Salmon Demes

Overall mating patterns in chum salmon demeS based upon size or age-at-maturity may occasionally be affected by the arrival and subsequent distribution of fish onto their spawning grounds. Hunter (1959), Mattson and Rowland (1963), Sano (1966), Bailey (1976), and Helle (1979) all observed that chum salmon originating from different brood years migrated into their natal streams at slightly different times. Such a propensity enhances the likelihood of an overall positive assortative mating pattern since fish with similar ages and presumably body sizes would arrive on a spawning ground at the same time.

Moreover, instream movements of spawners may also cause aggregations of fish having similar phenotypes. Larger and stronger individuals may be able to migrate over rapids or falls that smaller fish are unable to negotiate. Conversely, in periods of low stream flow, smaller fish may penetrate further upstream than larger individuals. Consequently, even if fish representing an array of brood years entered a stream simultaneously they may utilize different spawning areas.

The impact of such temporal and spatial factors on overall mating patterns in chum salmon demeS probably varies yearly and by population, but in most cases it should remain relatively unimportant. First, total temporal isolation of one age group from all the others spawning in the same stream rarely occurs, even in those streams where such tendencies

have been observed (see Helle 1979, Appendix 2). Other chum salmon populations may never exhibit these migration patterns. Table 1 for instance, shows that the age composition of chum salmon entering Big Beef Creek tends to remain fairly constant throughout a run. Second, even if fish arrive on a spawning ground at dissimilar times they may still be able to spawn with one another. Data gathered on fish placed in the experimental stream showed males would court and spawn with females for 10 to 18 days or throughout almost their entire spawning ground residency (Table 2). Consequently, the potential amount of gene exchange occurring among fish arriving into a stream at different times can be quite high.

Third, in North America, most of the chum salmon stocks south of Central Alaska spawn in short coastal streams. These fish usually mature and reproduce soon after reaching freshwater (Gilbert 1923; Neave 1966) and thus tend to breed in the first several kilometers of their natal streams. Helle (1979) for example, observed that 95% of the spawning area utilized by chum salmon returning to Olsen Creek (Prince William Sound, Alaska) was located in an intertidal stream channel. Spatial isolation based on size in such areas is improbable because up- or downstream movement is not hindered at high tide.

In coastal streams where intertidal spawning rarely occurs several factors other than body size appear to affect where chum salmon spawn. Hunter (1959) found that certain portions of Hooknose Creek (King Island, British Columbia) were consistently utilized while other adja-

Table 1. The age composition of chum salmon entering Big Beef Creek during 1971, 1974, 1975, and 1976*
by weekly periods - continued.

Brood year	Run	Weekly interval (Julian date)	Females					Males				
			%3	%4	%5	No. /wk	No. aged /wk	%2	%3	%4	%5	No. aged /wk
1974	Late	364-004	--	no data		2	0	--	no data		--	1
		005-011	"	"		0	0	"	"		"	0
		012-018	"	"		2	0	"	"		"	0
		019-025	"	"		1	0	"	"		"	0
1975	Early	252-258	.95	.05	.00	21	21	.00	.97	.03	.00	35
		259-265	.94	.06	.00	83	83	.04	.95	.01	.00	85
		266-272	.99	.01	.00	236	223	.01	.97	.02	.00	226
		273-279	.98	.02	.00	158	148	.01	.96	.03	.00	129
		280-286	.95	.05	.00	67	64	.00	.97	.03	.00	66
		287-293	1.00	.00	.00	30	29	.00	1.00	.00	.00	24
		294-300	1.00	.00	.00	6	6	.00	1.00	.00	.00	7
		301-307	.71	.29	.00	7	7	.00	.17	.66	.17	6
1975	Late	308-314	.50	.42	.08	12	12	.00	.52	.39	.09	23
		315-321	.36	.64	.00	16	11	.00	.50	.50	.00	15
		322-328	.22	.78	.00	36	36	.00	.25	.70	.04	27
		329-335	.15	.81	.03	59	59	.00	.33	.64	.03	74
		336-342	.20	.76	.04	51	51	.00	.24	.73	.03	79
		343-349	.31	.69	.00	66	64	.00	.27	.69	.04	51
		350-356	.32	.66	.03	39	38	.00	.37	.63	.00	30
		357-363	.56	.44	.00	16	16	.00	.64	.36	.00	23
		364-004	.61	.36	.02	44	44	.00	.68	.32	.00	26
		005-011	.55	.36	.09	12	11	.00	.77	.23	.00	13
		012-018	.00	.00	.00	0	0	.00	.00	.00	.00	0
		019-025	.50	.50	.00	2	2	.00	.00	1.00	.00	3

Table 1. The age composition of chum salmon entering Big Beef Creek during 1971, 1974, 1975, and 1976*
by weekly periods - continued.

Brood year	Run	Weekly interval (Julian date)	Females					Males					
			%3	%4	%5	No. /wk	No. aged /wk	%2	%3	%4	%5	No. /wk	No. aged /wk
1976	Early	245-251	.00	1.00	.00	12	12	.00	.00	1.00	.00	20	19
		252-248	.05	.95	.00	116	115	.00	.04	.96	.00	154	147
		259-265	.08	.92	.00	203	203	.00	.12	.88	.00	130	120
		266-272	.25	.75	.00	121	121	.02	.17	.81	.00	103	103
		273-279	.27	.73	.00	137	137	.02	.39	.59	.00	47	46
		280-286	.30	.70	.00	77	77	.00	.41	.59	.00	41	39
		287-293	.21	.79	.00	19	19	.00	.00	1.00	.00	4	3
	294-300	.39	.61	.00	39	39	.00	.30	.70	.00	30	30	

*The fish returning in these runs were the experimental animals used in the mate selection experiments.

Table 2. Field data gathered in the experimental stream illustrating the length of time male chum salmon remain sexually active.

Male no.*	Body weight (kg)	Total freshwater longevity (days)	No. of days was sexually active (courted ♀♀)**	% of freshwater life-time male was sexually active
13	5.245	16	13	.81
15	5.330	12	11	.92
10	4.536	13	12	.92
26	5.557	8	7	.88
14	6.464	14	12	.86

*These fish competed against other males for females but were provided with potential mates throughout their entire freshwater life-times.

**A male was considered sexually active if he adopted the "alpha" or "satellite" reproductive strategy.

cent areas were not. Apparently, where a female spawns is influenced by water depth, velocity, the occurrence of upwelling or accelerating flows, gravel composition (Sano 1966; Hoopes 1972; Tautz and Groot 1975; Duker 1977; Graybill 1978), and whether a site is guarded by other females (Mathisen 1955; Schroder 1973). A study by Duker (1977) showed that chum salmon females from the same stock constructed nests in similar types of gravel, regardless of their body size. Since the gravel composition of a streambed is affected by stream velocity, width, gradient, and flow (Hoopes 1972) these results imply that fish of various sizes prefer spawning sites with similar hydrological characteristics.

The length of time a female migrates or remains in freshwater before she begins to search for a territory location is undoubtedly associated with her sexual maturity. Developing salmon eggs are sensitive to mechanical shock until blastopore closure (≈ 144 T.U. °C, Smirnov 1955) and consequently, the longer a female can protect her eggs from being dislodged by other fish, the greater the probability her eggs will survive to produce fry. Thus, a mature female should quickly take possession of a spawning site, mate, and guard her eggs for as long as possible. Since female chum salmon returning to coastal streams are usually mature, and prefer to spawn in similar areas, it is likely that females with different body sizes will often spawn in close proximity to one another.

The reproductive activities of males also increase the likelihood that fish with different body sizes will be found in the same spawning

areas. Males neither prepare nests nor protect recently buried eggs; free of this kind of parental investment a male's potential fitness depends primarily on his ability to fertilize eggs. To accomplish this task males remain reproductively active for long periods of time and move up- and downstream in search of females. In fact, a tagging experiment in Traitor's River (Mattson et al. 1964) showed that chum salmon males commonly moved 180 to 360 m and in one case 1.8 km (the length of the spawning ground) after becoming sexually mature. The tendency to search for females increases the chance that males with different body sizes or ages will randomly distribute themselves throughout a spawning ground.

Fourth, the chum salmon that return to a major river system usually represent a variety of stocks (Gilbert 1923; Smirnov 1975; Birman 1977). The fish in such stocks, like those returning to smaller streams will return to particular portions of a watershed to breed (Birman 1956, as cited by Birman 1977). These traditional spawning areas may be very different from one another; for instance, some may be located in limnocrenes, others in areas of fast current and so on (Smirnov 1975). Regardless of where a stock spawns all of its members should reach sexual maturity at approximately the same time. For plainly, it does not pay a semelparous organism of either sex to reach maturity before or after most of its contemporaries. As we have seen, when a chum salmon reaches maturity, its location within a spawning ground should be governed largely by the presence of desirable resources (i.e., spawning sites, potential mates, etc.) and not by its absolute size. Consequently, it is

clear that fish of various sizes or ages will probably mate randomly with one another unless sexual selection intervenes.

The Overall Mating Patterns Observed in the Experimental Stream

The reproductive tactics of each sex (cf., Fig. 2) make the likelihood of sexual selection, particularly intrasexual competition, very great. Male competition for females is expected to escalate as a spawning season progresses because females remain sexually active for much shorter periods of time than males. Most of the females placed into the experimental stream successfully buried all of their eggs within 30 to 40 hr after starting their first nest (Fig. 6). Assuredly, female and male competition for space and mates, intrinsic differences among stocks, and climatic factors may alter the amount of time a female spends on egg deposition. However, observations made in the experimental stream under varying climatic and social circumstances showed that the longest time a female spent constructing her nests was 93 hr. This is still only one-third as long as most males remain sexually active (cf., Table 2).

Figure 7 illustrates the increase in the number of sexually active males/"active" female (OSR) in one section of the experimental stream. In spawning areas where fish arrive on a continuous basis the OSR must correspondingly increase although probably not in such a dramatic manner. The influence that such skewed sex ratios have on overall mating patterns depends on how males compete among themselves for females and whether either sex possesses a tendency to prefer mates with certain phenotypic traits. For example, regardless of the OSR in a deme the

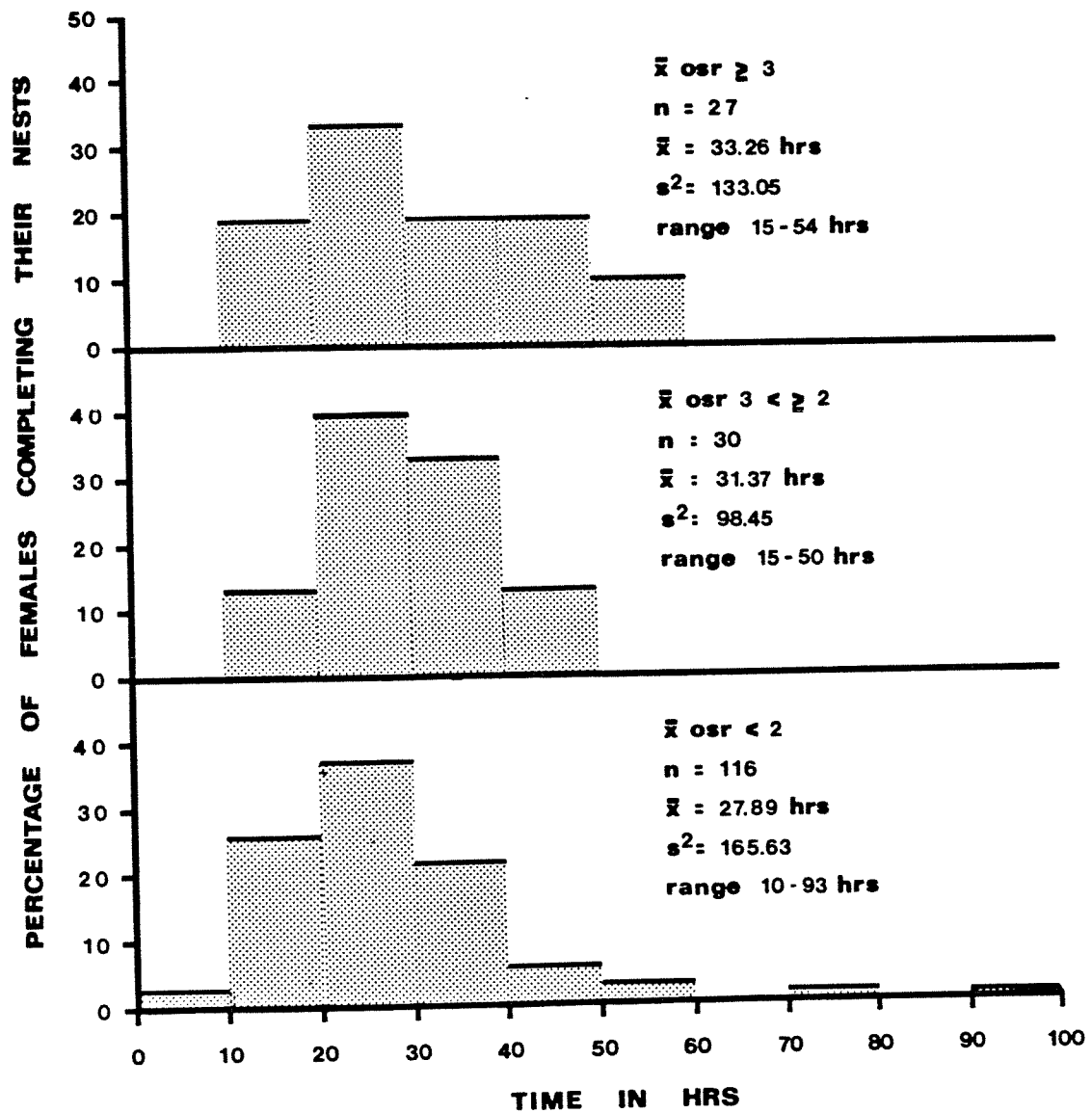


Fig. 6. The amount of time required by female chum salmon to complete all their nests under different Operating Sex Ratios.

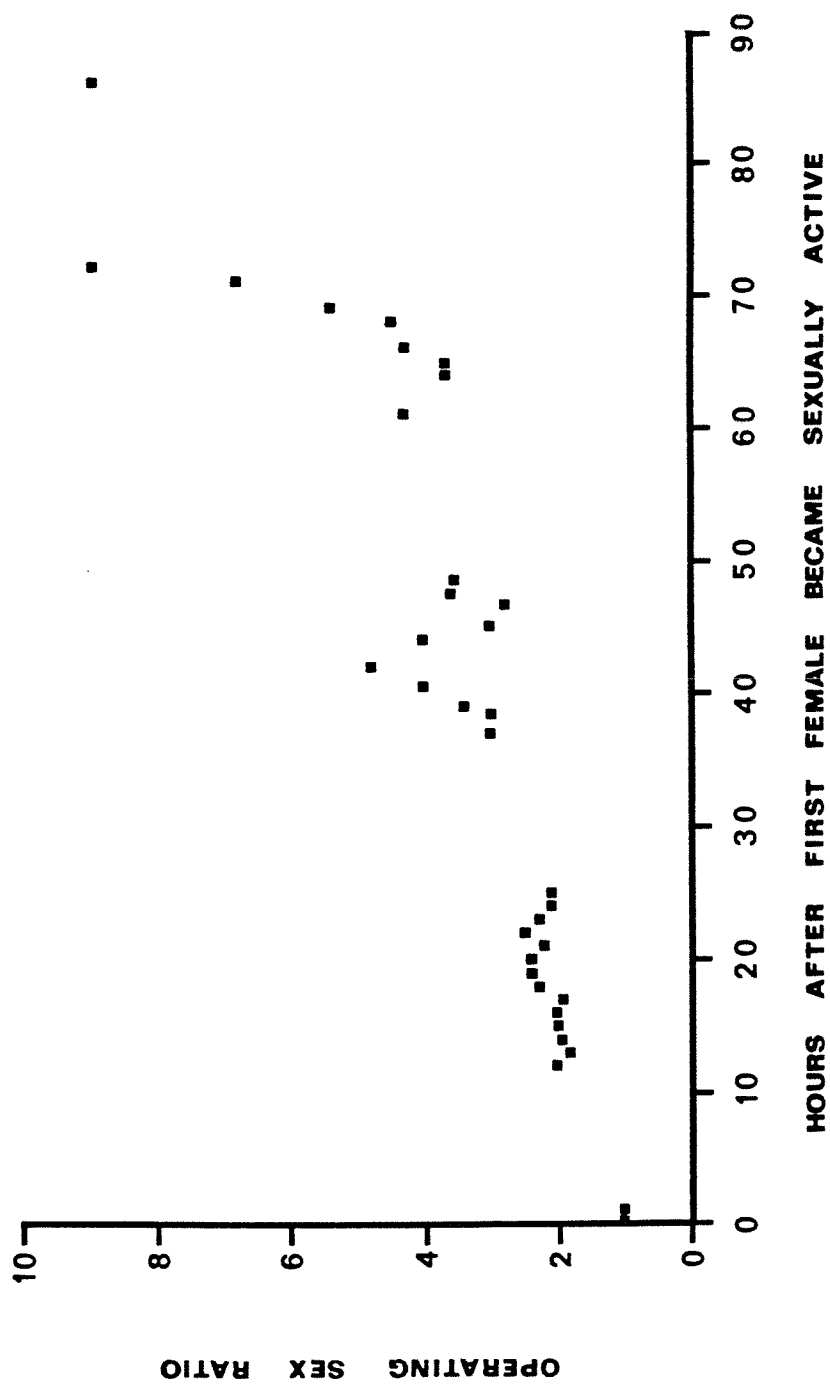


Fig. 7. Temporal changes in the number of sexually active males/females (OSR) in a section of the experimental stream that had a tertiary sex ratio of two males/female.

overall mating pattern could be random if mate choice is determined entirely on a "first-come first-served" basis. Moreover, a nonrandom mating pattern could consistently manifest itself in demes with different OSRs if one or both sexes select mates on the basis of body size or some other variable phenotypic trait. However, if ritualized fighting or simple aggression play important roles in determining which males have access to females, then the OSR of a deme may have profound effects on who spawns with whom.

Fish were placed into 17 sections of the experimental stream to ascertain whether overall mating patterns remained the same or varied under different OSRs. The age composition and weight range of these fish, how often they were observed, and the mean OSR of each population is presented in Table 3. A representative sample of the overall mating patterns observed in these sections is depicted in Fig. 8. This figure shows that when the OSR was ≤ 1 pairing was essentially random. To clarify what occurred at higher OSRs the number of expected and observed pairs that had "low," "medium," and "high" weight ratios ($\sigma^{\uparrow} \text{wt} : \phi \text{ wt.}$) in seven sections of the experimental stream are shown in Table 4.

The data in this table and in Fig. 8 illustrate that when OSRs are ≥ 1.4 , pairs with relatively low size ratios occur less often than expected (Fig. 8c). Moreover, at relatively high OSRs (≥ 3) most of the observed pairs had size ratios in the upper third of those possible (Fig. 8e,f). Clearly, these fish are not pairing randomly when the OSR exceeds 1, nor are they consistently, if ever, pairing in a positive

Table 3. Biological and observational data on the chum salmon placed into the experimental stream to examine the influence of various OSRs on overall mating patterns.

Experimental stream population	Year	Run	Tertiary sex ratio (♂:♀)	$\bar{x}$ Operating sex ratio	No. of times obs.	No. of pairs obs.	Female age and wt composition					Male age and wt composition				
							%3	%4	%5	Wt range in kg	Wt	%2	%3	%4	%5	Wt range in kg
C-3	1974	Early	6:8	0.92	17	79	1.00	.00	.00	3.1-5.8	.00	.00	.83	.17	.00	3.4-6.7
C-7	1974	Early	7:6	2.97	36	78	1.00	.00	.00	2.9-3.9	.00	.00	.86	.14	.00	3.9-6.8
C-5-A	1974	Late	26:29	1.43	14	87	.07	.93	.00	3.1-5.7	.00	.00	.15	.77	.08	2.7-7.6
C-5-B	1974	Late	30:30	1.80	15	135	.20	.73	.07	3.4-6.5	.00	.00	.10	.83	.07	3.3-7.3
C-9	1974	Late	25:13	2.01	13	113	.08	.84	.08	3.0-6.9	.00	.00	.08	.88	.04	2.4-7.3
C-6	1974	Late	28:14	2.28	12	93	.29	.71	.00	2.9-5.0	.00	.00	.29	.71	.00	2.9-6.6
C-5	1975	Early	8:17	0.98	38	127	1.00	.00	.00	2.3-4.1	.00	.00	1.00	.00	.00	3.7-5.3
C-11	1975	Early	8:14	1.05	28	131	.93	.07	.00	2.6-4.4	.00	.00	1.00	.00	.00	2.9-4.8
C-6	1975	Early	20:20	1.18	12	143	.80	.20	.00	2.3-4.1	.00	.00	.95	.05	.00	2.7-4.9
C-7	1975	Early	16:30	1.22	19	145	1.00	.00	.00	2.3-4.4	.00	.00	1.00	.00	.00	2.6-4.5
C-3	1975	Early	22:21	1.69	26	152	1.00	.00	.00	2.3-4.8	.10	.00	.85	.05	.00	2.3-4.8
C-9	1975	Early	29:15	2.19	17	87	1.00	.00	.00	2.7-4.1	.00	.00	1.00	.00	.00	2.6-4.8
C-10	1975	Early	23:9	3.83	22	102	1.00	.00	.00	2.2-4.0	.05	.00	.90	.05	.00	2.1-4.8
C-4	1975	Late	11:13	1.41	18	119	.08	.92	.00	2.7-5.2	.00	.00	.45	.45	.10	3.7-6.7
C-3	1976	Early	17:15	1.84	28	171	.00	1.00	.00	2.7-5.8	.00	.00	.06	.94	.00	3.6-7.4
C-10	1976	Early	32:9	3.23	20	69	.11	.89	.00	3.2-5.1	.00	.00	.00	1.00	.00	4.0-7.5
C-4	1976	Early	32:16	3.98	50	237	.00	1.00	.00	3.2-5.6	.00	.00	.06	.94	.00	1.6-7.8

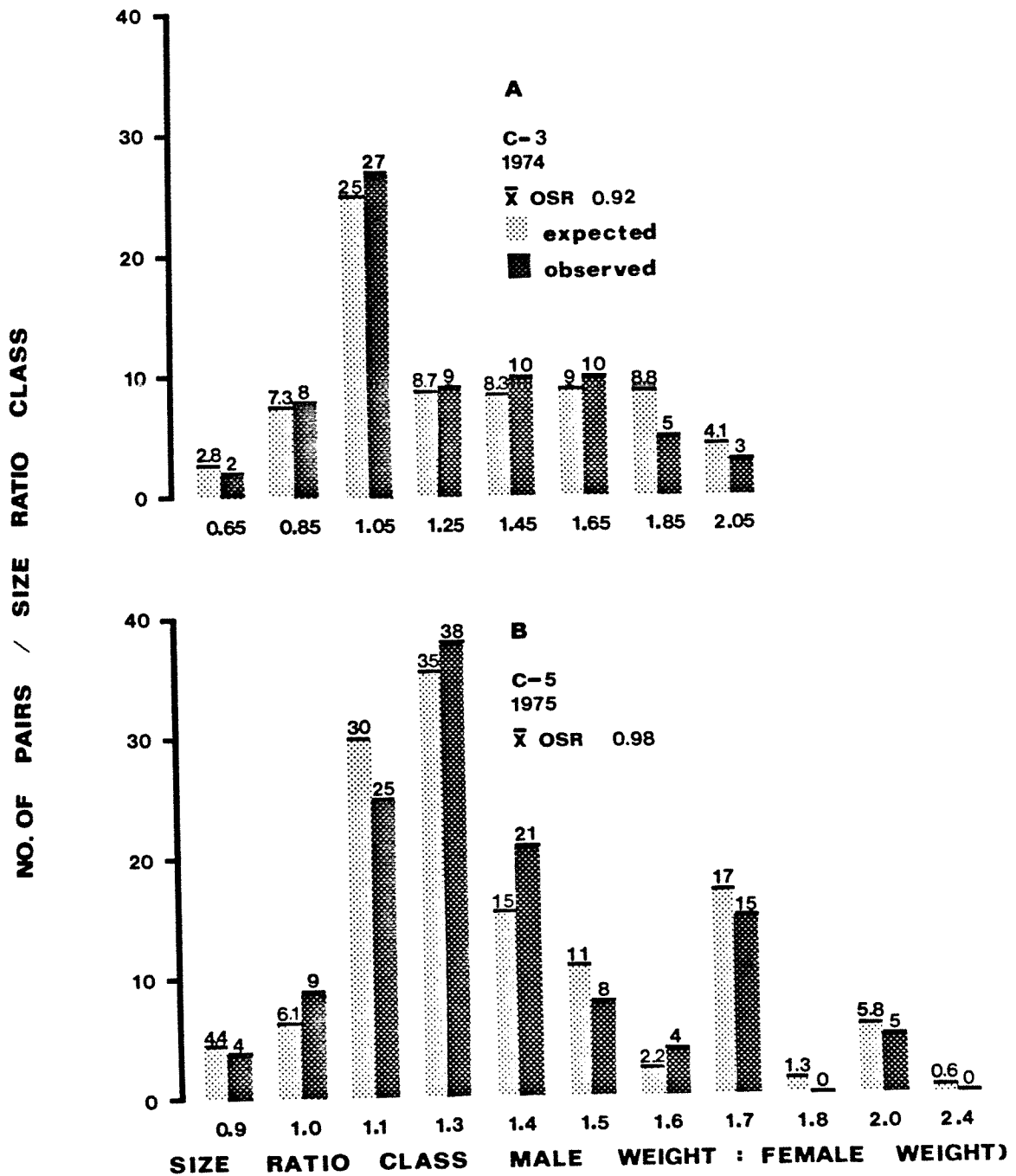


Fig. 8. The expected (random) and observed number of chum salmon pairs falling into various size ratio classes (male wt: female wt) in six sections of the experimental stream.

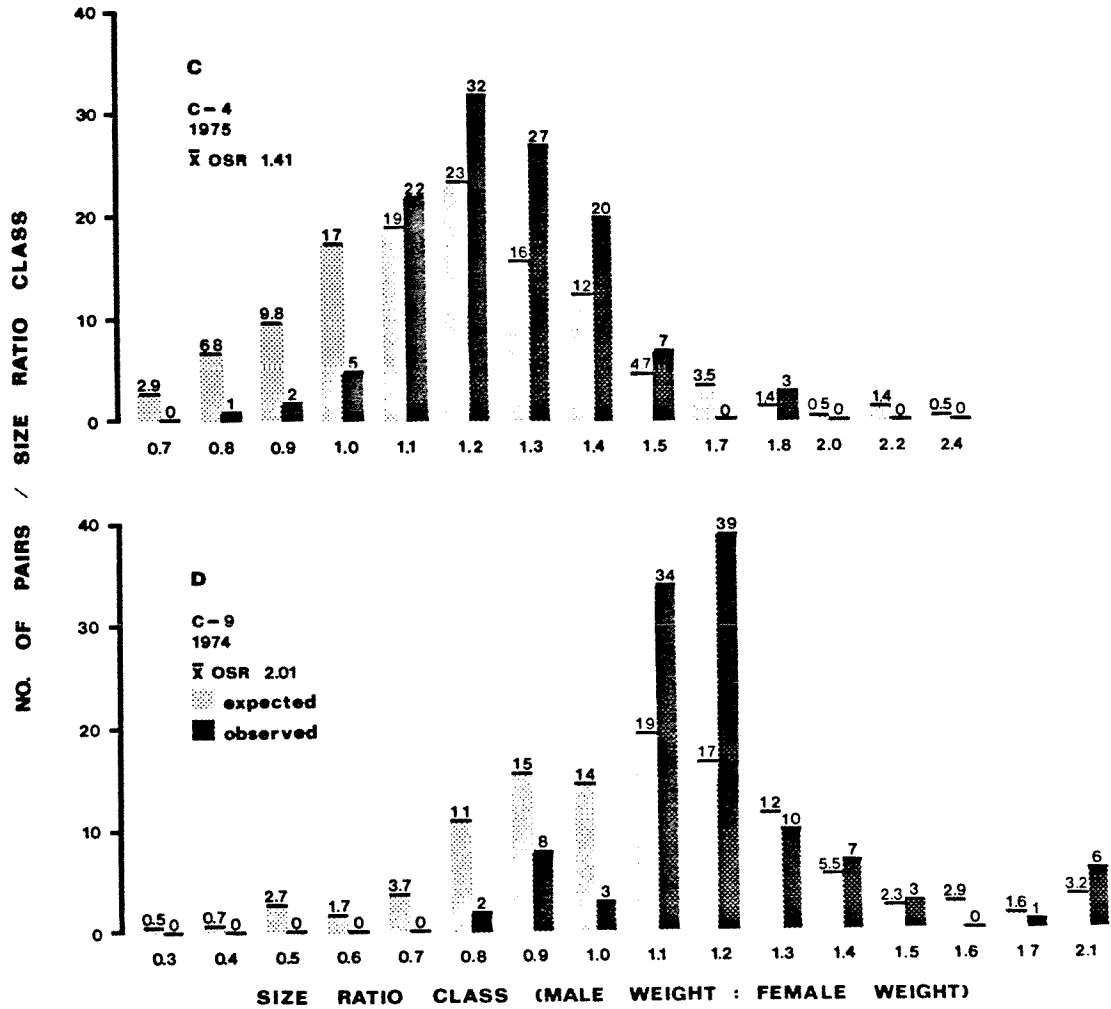


Fig. 8. The expected (random) and observed number of chum salmon pairs falling into various size ratio classes (male wt: female wt) in six sections of the experimental stream - continued.

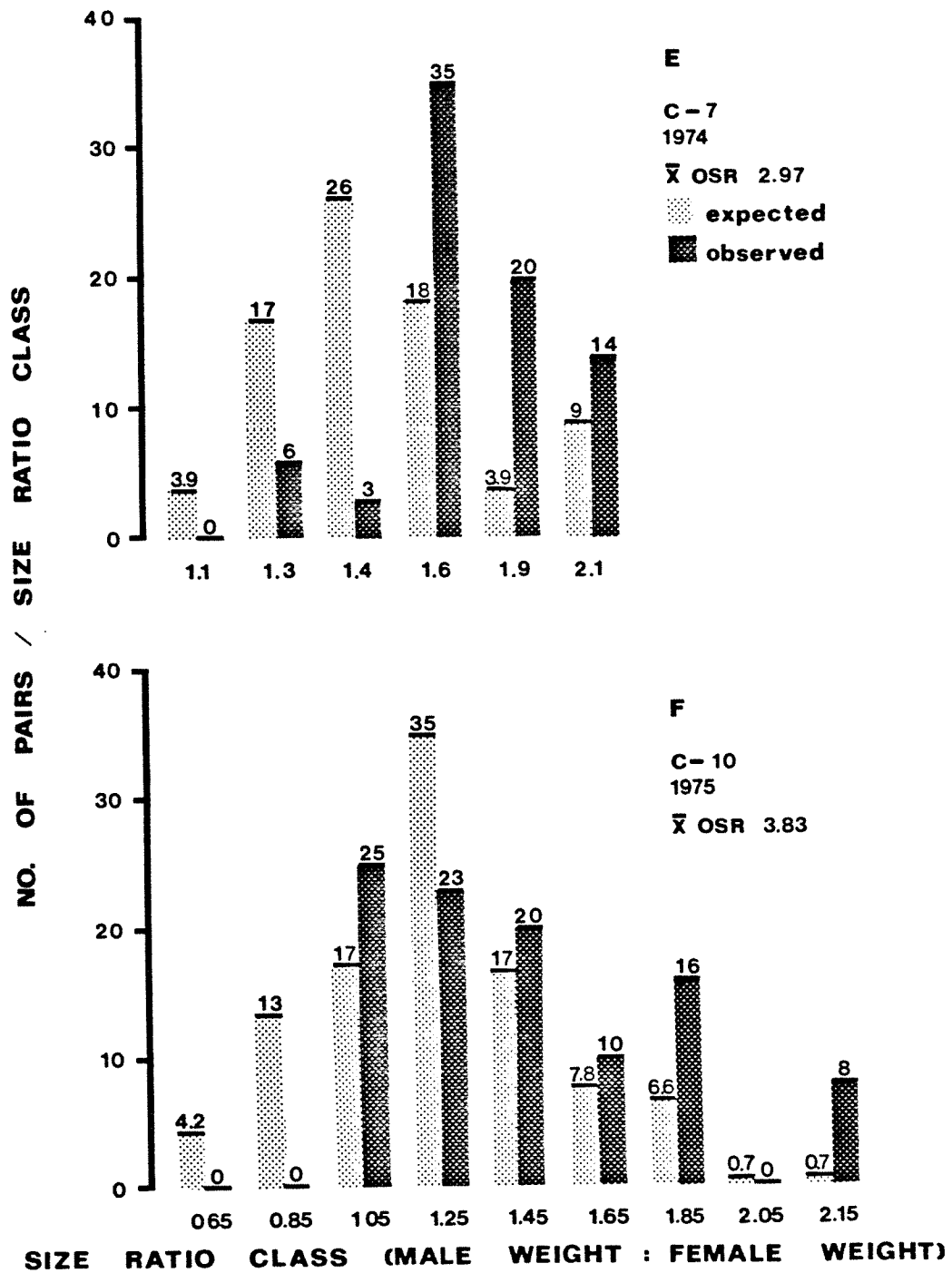


Fig. 8. The expected (random) and observed number of chum salmon pairs falling into various size ratio classes (male wt: female wt) in six sections of the experimental stream - continued.

Table 4. The number of observed and expected pairs falling into "low," "middle," and "high" weight ratio classes that occurred in seven sections of the experimental stream.

Section	OSR	No. of pairs/size ratio class (σ wt.: ♀ wt.)								Total pairs
		Lower third		Middle third		Upper third				
		Observed	Expected	Observed	Expected	Observed	Expected			
C-3	0.92	25.74	~ 24.67	26.91	~ 24.67	21.35	~ 24.67	74		
C-5	0.98	40.68	~ 43.00	49.16	~ 43.00	39.16	~ 43.00	129		
C-4	1.41	11.44	< 39.67	50.97	> 39.67	56.59	> 39.67	119		
C-3	1.84	26.15	< 57.33	51.39	~ 57.33	94.46	> 57.33	172		
C-9	2.01	10.43	< 37.67	50.98	> 37.67	51.59	> 37.67	113		
C-7	2.97	6.60	< 26.00	12.26	< 26.00	59.14	> 26.00	78		
C-10	3.83	24.12	< 34.00	22.90	< 34.00	54.98	> 34.00	102		

assortative fashion. Instead, overall mating patterns appear to vary with the OSR occurring within a breeding population.

The Effects of Sexual Selection on Males

The studies that examined male and female intrasexual competition and epigamic selection were performed to determine the importance of these factors on the creation of the overall mating patterns observed in the experimental stream. Intrasexual competition among males for mates appears to be the most important factor affecting these patterns.

The average amount of time that "small," "medium," and "large" males (cf., p. 32) spent as alpha males under various OSRs is depicted in Fig. 9. One-way ANOVAs and Newman-Keuls multiple range tests were performed on these data (Table 5), and showed that males in all three size classes had equal access to females when the OSR was ≤ 1.4 . As the OSRs increased the relative size of a male became more important. For example, when the OSR exceeded 1.4 but was less than 2 "large" and "medium" sized males usually spent more time courting females than "small" ones. When competition for females became more intense (OSR ≥ 3) the largest males in a deme had a decided advantage over their smaller rivals. However, the amount of time these animals spent courting females also decreased at the highest OSRs observed (see Fig. 9). This is to be expected, because at these OSRs "large" males regularly competed among themselves, rather than against smaller rivals, for the relatively few females that were available. Consequently, one possible reason that pairs with low size ratios become scarce at high OSRs is simply that

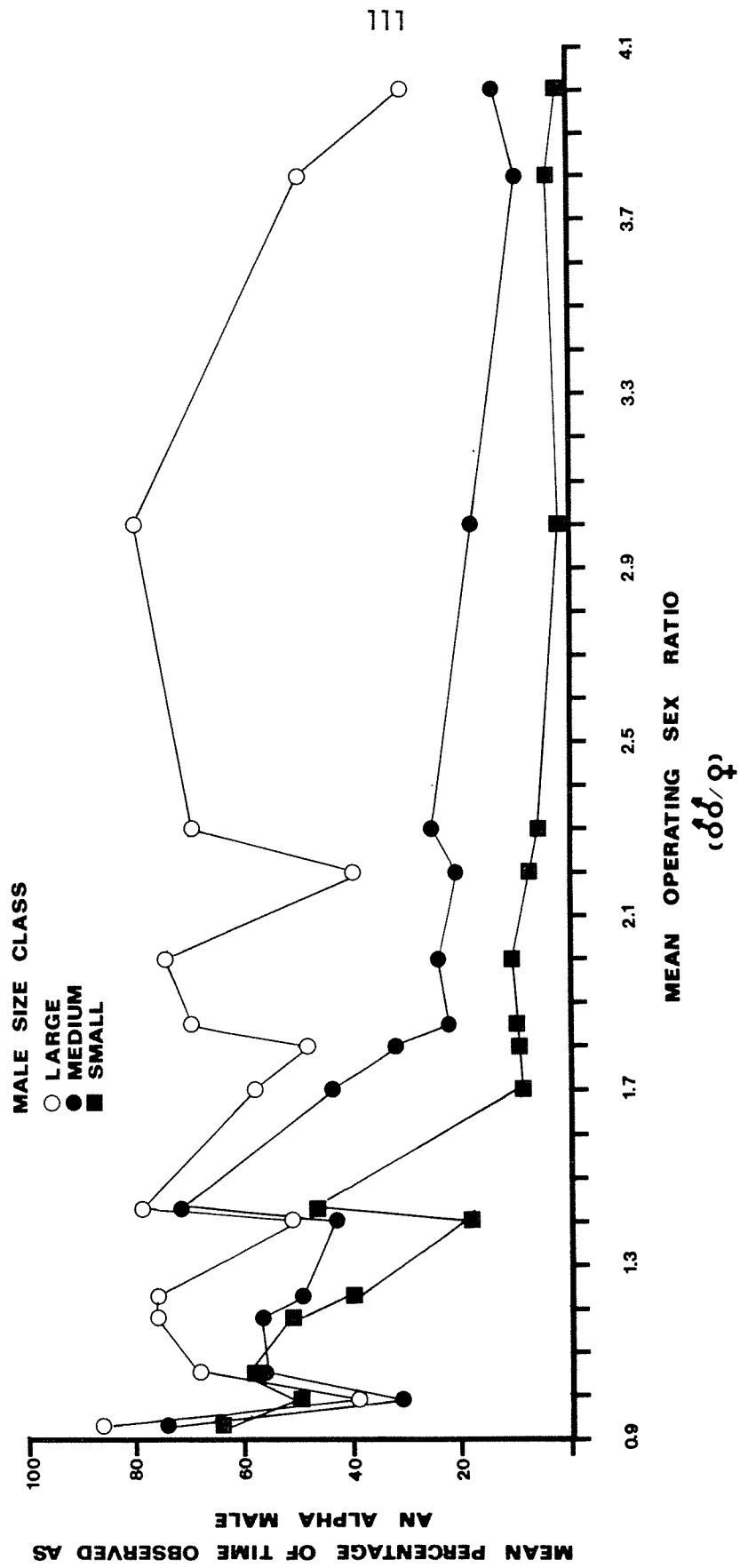


Fig. 9. The average amount of time that "small," "medium," and "large" males spent as alpha males under various Operating Sex Ratios.

Table 5. Results of the tests used to determine whether "small," "medium," and "large" males had equal opportunities to court females under different OSRs.

Population	$\bar{x}$ OSR	Total no. of $\sigma\sigma$ in the population	One-way ANOVA F statistic	Decision on H_0^* ($\alpha=0.05$)	Results of the Newman-Keuls multiple range tests		
					Sm $\sigma\sigma$	Med $\sigma\sigma$	Lg $\sigma\sigma$
C-3 1974	0.92	6	1.95	Accept			
C-5 1974	0.98	8	0.46	"			
C-11 1975	1.05	7	0.10	"			
C-6 1975	1.18	19	1.20	"			
C-7 1975	1.22	16	2.96	"			
C-4 1975	1.41	11	8.42	Reject			
C-5-1 1974	1.43	26	2.96	Accept			
C-3 1975	1.69	19	10.40	Reject			
C-5-2 1974	1.80	30	15.86	Reject			
C-3 1976	1.84	16	13.06	Reject			
C-9 1974	2.01	24	14.77	Reject			
C-9 1975	2.19	24	6.29	Reject			
C-6 1974	2.28	27	22.34	Reject			
C-7 1974	2.97	6	11.04**	Reject			
C-10 1975	3.83	21	7.40	Reject			
C-4 1976	3.98	27	90.21	Reject			

* H_0 : Males in all three size classes have an equal opportunity to court females.

** $\alpha = .10$ because of small n

smaller males cannot successfully defend the females they find nor seize females from males that are already courting them.

The Importance of Male Size and Physical Condition in Intrasexual Combat

Male chum salmon use physical force, i.e., open mouthed rushes, bites, and body blocks to exclude or usurp sexual rivals from potential mates. Occasionally these simple confrontations escalate into ritualized battles complete with stereotypic displays (Fig. 10). When this happens the males perform a "lateral display" by lying motionless and parallel to one another with their dorsal fins fully raised. One of the males will then slowly swim about a meter upstream, turn laterally and display his side. The downstream fish may then attack the displayed side or remain stationary. If the displaying male is not attacked he may thrust his caudal fin under his rival's head and repeat the above "T" display or drift further downstream and attack the side of his motionless opponent (Schroder 1973).

During an attack a fish hurls himself towards his rival with powerful strokes of his caudal fin. His mouth is often widely agape and if he can grasp a fin or portion of his opponent's body he will shake his head rapidly back and forth. Each attack lasts for several seconds and after it is completed both males return to the nest site of the contested female and resume the lateral display. Shortly thereafter one of the males will move upstream and perform another "T" display. This sequence of displays and attacks may last for several hours or more.

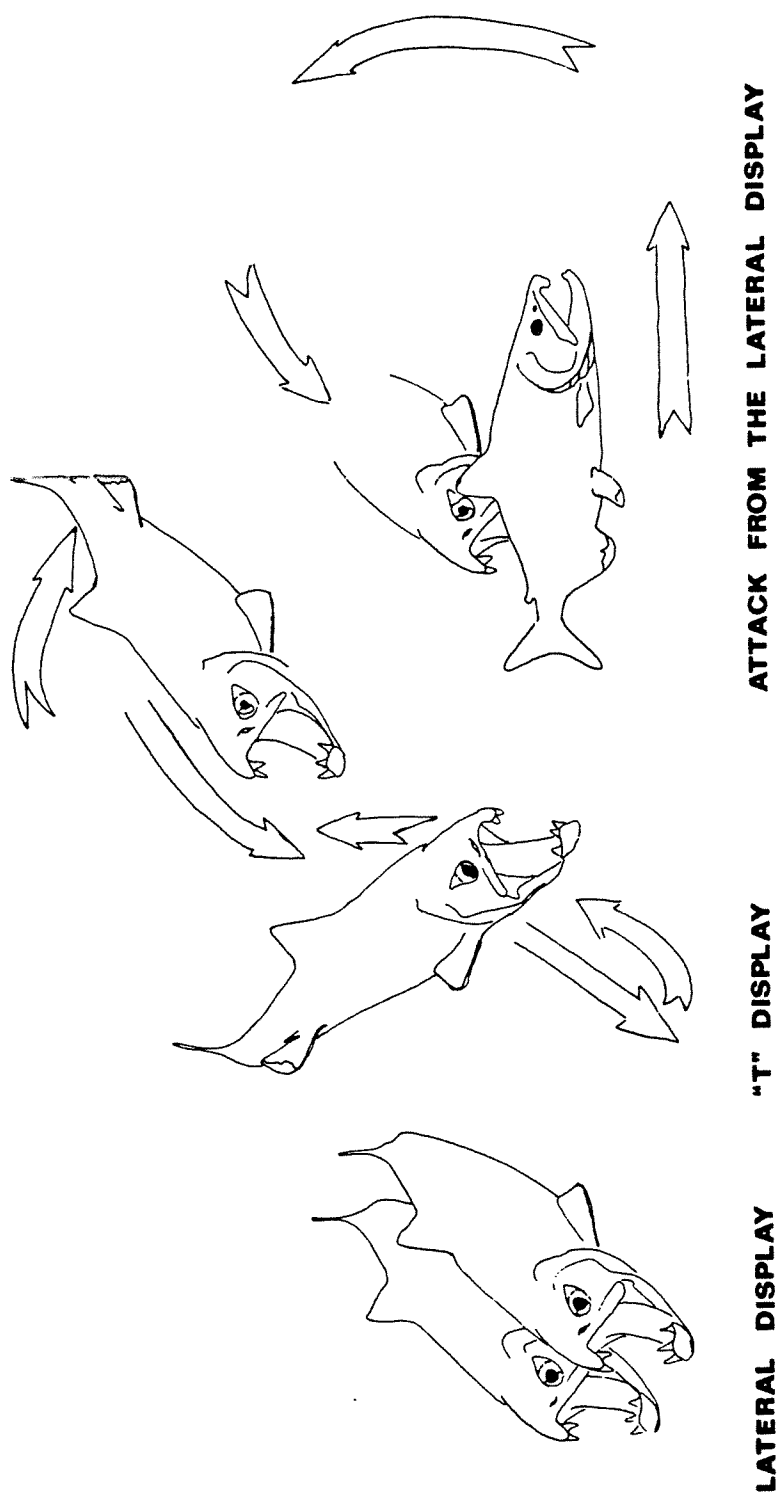


Fig. 10. Ritualized fighting displays used by male chum salmon. See text for further details.

The ability of a male to win these contests and otherwise defend his potential mates depends in part on his size and physical condition. I attempted to determine the relative importance of these two factors on male dominance by artificially arranging confrontations between males that were larger than their opponents but in poorer physical condition (cf., pp. 33-34). Five males ("residents") were held in the experimental stream and forced, on a daily basis, to compete against smaller opponents that had recently entered freshwater. The data presented in Table 6 show that for approximately 70% of their reproductive lifetimes the "resident" males dominated opponents that were nine-tenths their size. As these fish neared death their ability to defeat smaller opponents slowly decreased. Thus, it appears that the relative size of a male plays an important role in determining how many sexual rivals he will be able to dominate throughout his reproductive life.

The behavioral observations made on the "resident" males and their smaller "challengers" also revealed that if one individual was clearly dominant, the weaker animal would usually attempt to escape. Since this was impossible in the experimental stream, the subdominant males would lower their heads into the substrate, raise their tails, and remain quiescent except for slight movements from their operculums. While in this posture, which was commonly maintained for hours, they remained fairly immune from attack. McCart (1970) noticed a very similar "submissive posture"⁶ in sockeye salmon while he was observing male intra-sexual competition in small, enclosed "pens." Under natural spawning

Table 6. The effect of freshwater residency on the ability of chum salmon males to dominate smaller opponents who have just migrated onto a spawning ground.

Tag no. of resident male	Body wt in kg	No. of days alive	Total no. of challengers faced	Percentage of the resident male's reproductive lifetime that he was dominant over smaller, newly arriving challengers						
				Relative size of challenger males						
				1.0-.9	.89-.80	.79-.70	.69-.60	.59-.50	.49-0	
14	6.46	14	13	55	55	55	55	69	83	
26	5.55	8	8	83	95	95	95	95	95	
15	5.33	12	13	80	80	80	89	89	96	
13	5.24	16	15	67	67	67	73	73	79	
10	4.54	13	12	74	74	82	82	97	97	
$\bar{x}$ or Σ			$\Sigma 61$	$\bar{x}$	72	74	76	79	84	90

conditions this display probably rarely occurs because weaker males should be able to swim away from their stronger antagonists.

If the difference in strength between a "resident" and "challenger" was not as great as above, then the subdominant male would position himself in back of the alpha male and become a satellite to the courting pair. Ritualized fights occurred only when the males were equally matched. McCart (1970) observed that "large" sockeye males commonly ignored the lateral displays presented to them by smaller opponents. While my "resident" males were in good physical condition they either did the same thing or attacked their smaller opponents without performing a "T" display (see Fig. 10). However, as they grew weaker, ritualized contests between "resident" males and "challengers" one half their weight did occur. This suggests that males use factors besides absolute mass to assess the relative strength of their rivals. Perhaps how easily a male can be pushed, the strength of his blows or color pattern (see pp. 129-136) convey information about his tenacity and vigor to sexual rivals.

The Occurrence and Gametic Success of Satellite Males in Chum Salmon Demes

Once a male has been dominated he may either leave and search for other females or remain as a satellite. Contrary to the above observations which were made in confined areas (1.5 x 3.0 m sections of the

⁶Dead salmon often assume this posture and consequently this display may be an attempt to mimic a carcass rather than an effort to communicate submissiveness.

experimental stream), relatively weak males may adopt this strategy since under more spacious conditions they can evade the repeated attacks of an opponent. Moreover, as the OSR of a deme increases the ability of a male to totally dominate a rival also diminishes because he usually has to simultaneously contend with more than one opponent.

Ecological theory predicts that as male intrasexual competition escalates the occurrence of satellite males will increase. Data gathered in the experimental stream and presented in Fig. 11 corroborate this contention. The figure shows that the percentage of sexually active males utilizing this strategy was nearly zero when the OSR was ≤ 1.4 but was approximately 20% at higher OSRs.

The number of satellite males associated with a pair remained surprisingly constant throughout the range of OSRs examined (Table 7). However, the percentage of pairs within a deme accompanied by satellites rose in an almost linear fashion as the OSR increased (Fig. 12). These data suggest that if a male is dominated by two or three sexual rivals he tends to leave a female rather than stay and occupy a subordinate position.

There are two reasons for this behavioral trend. First, while a female constructs a nest she continually broadcasts information about her reproductive status (cf., pp. 146-159). The closer a male can locate himself to an "active" female the greater the likelihood he will be able to perceive this information and act in an appropriate manner. Both McCart (1970) and Schroder (1973) observed that dominance hierarchies

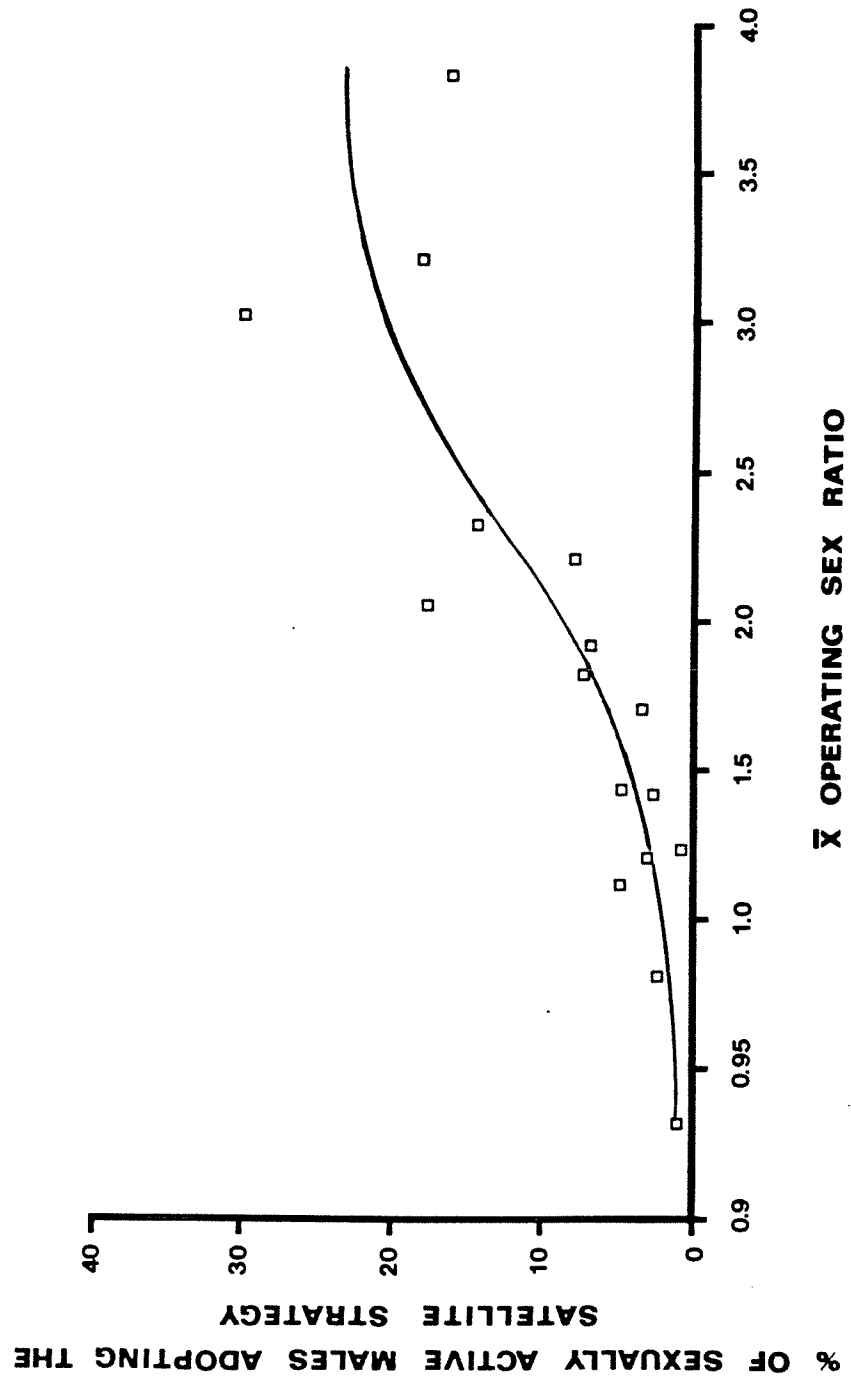


Fig. 11. The percentage of sexually active chum salmon males within demes having different OSRs that adopted the "satellite" strategy.

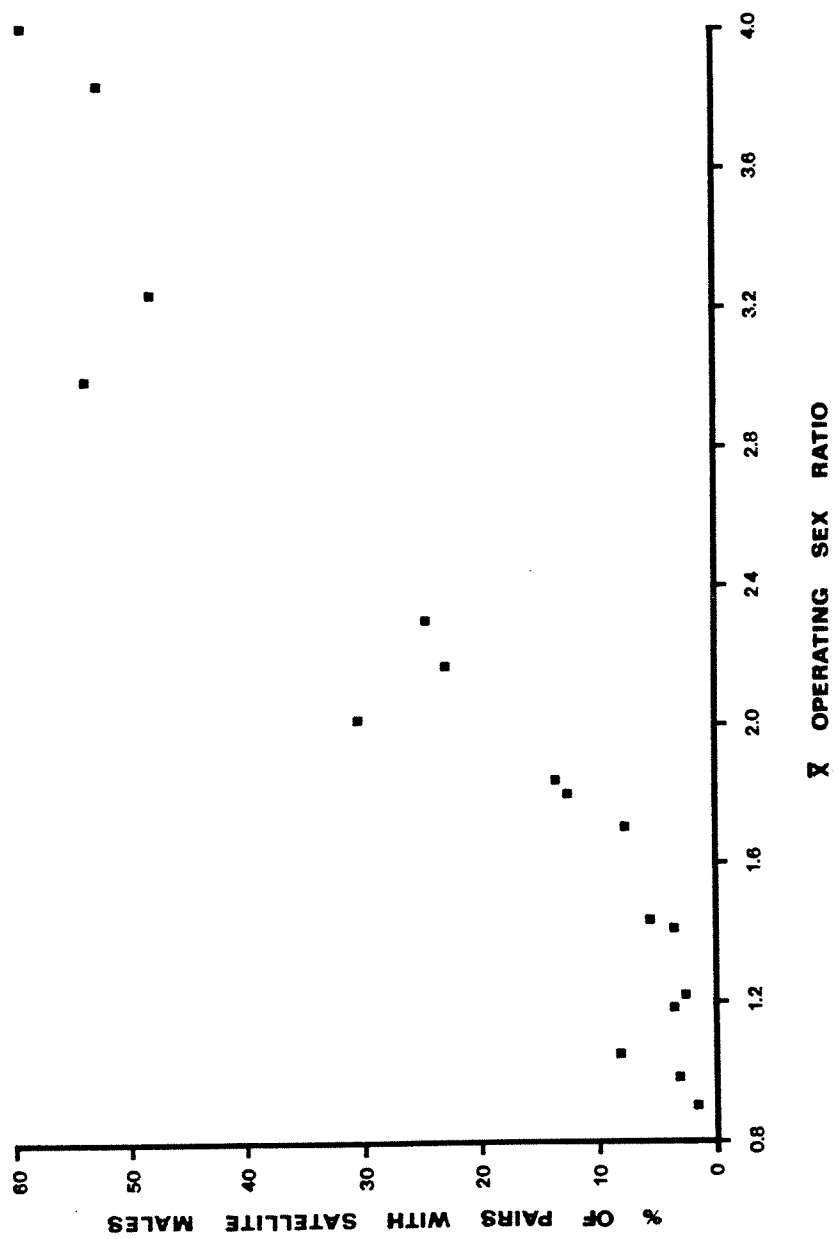


Fig. 12. The percentage of chum salmon pairs with satellite males at different OSRs.

Table 7. The number of satellite males associated with spawning pairs of chum salmon under different OSRs.

Section	$\bar{x}$ OSR	Total no. of pairs observed with satellite males	$\bar{x}$ of satellites around each pair	S.D.	Range
C-3 1974	.92	1	1.0	-	1
C-5 1975	.98	4	1.5	1.0	1-3
C-11 1975	1.05	8	1.0	0.0	1
C-6 1975	1.18	5	1.0	0.0	1
C-7 1975	1.22	4	1.0	0.0	1
C-4 1975	1.41	4	1.3	0.5	1-2
C-5-1 1974	1.43	5	1.6	0.9	1-3
C-3 1975	1.69	12	1.2	0.5	1-3
C-5-2 1974	1.80	17	1.4	0.9	1-4
C-3 1976	1.84	23	1.3	0.5	1-2
C-9 1974	2.01	36	1.8	1.4	1-7
C-9 1975	2.18	20	1.4	0.6	1-3
C-6 1974	2.28	23	1.4	1.0	1-5
C-7 1974	2.97	39	1.8	0.8	1-4
C-10 1976	3.23	33	1.6	1.0	1-4
C-10 1975	3.83	42	1.6	0.7	1-3
C-4 1976	3.98	99	1.6	1.0	1-5

exist among satellite males. The weakest fish in these temporary social systems are forced to the rear, and to one side of the pair. Thus, under some circumstances it may pay a relatively weak male to continue to search for a mate, rather than stay in a position where information vital to his potential fitness is obscured by competitors.

Second, even if a subordinate male can detect when a female begins to spawn, his chances of fertilizing any of her eggs is probably affected by the number and position of the males competing against him. Intuitively, one would expect that males lying on the peripheral edges of spawning groups would fertilize few if any eggs. Therefore, sperm competition may, like occlusion of behavioral cues, prompt relatively weak males to abandon highly contested females.

During a spawning act the female and alpha male lie tightly parallel to one another with their mouths widely agape. If satellite males are present, the most dominant one will position himself in a similar manner on the opposite side of the female. Additional satellites either lie adjacent to these males, or more commonly, attempt to stop the spawning act by pushing or lifting the female out of her nest depression. Similar interruptions are also caused by alpha males. In their efforts to attack male competitors they regularly dislodge females from their nests just before egg deposition occurs. These behavior patterns suggest that subordinate individuals may fertilize a portion of the eggs deposited during any given spawning act.

To estimate the gametic contributions of alpha and satellite males horizontal starch gel electrophoresis was utilized. Ten groups of fish consisting of one female and two or three males were placed into the viewing chamber and allowed to spawn. Videotape films were made of the fish and used with field observations to determine the dominance relationships among the males.

The males that competed for each female possessed different allozyme phenotypes. For example, in those cases where there were two males, one had the AAAa banding pattern of AAT while the other had the homozygous form. In the one instance where three males spawned simultaneously with a female each male had a different combination of AAT and PMI banding patterns (Table 8). All the females used in the experiment had homozygous banding patterns in both of these isozyme systems.

Thus, by analyzing some of the progeny produced from each spawning it was possible to estimate the percentage of eggs each male fertilized. Figure 13 presents the results of the biochemical analyses performed on the progeny and shows that under some circumstances, satellite males can make significant gametic contributions. Moreover, once these data were coupled with the behavioral observations made while the fish spawned, it was clear that the closer and more attuned a male was to the female the more eggs he was able to fertilize.

It would be inappropriate to conclude that all satellite males are as successful as those shown in Fig. 13. In the above experiment, alpha males were able to prevent their sexual rivals from spawning four out of

Table 8. The allozyme banding patterns of the male chum salmon used to estimate the gametic contributions of alpha and satellite males during natural spawning acts.

Spawning	Alpha male	Satellite 1	Satellite 2
1	Homozygous AAT*	Heterozygous AAT	
2	Homozygous AAT	Heterozygous AAT	Heterozygous AAT
	Homozygous PMI**	Heterozygous PMI	Homozygous PMI
3	Homozygous AAT	Heterozygous AAT	
4	Heterozygous AAT	Homozygous AAT	
5	Homozygous AAT	Heterozygous AAT	
6	Heterozygous AAT	Homozygous AAT	

*AAT = Asparate aminotransferase

**PMI = Phosphomannose isomerase

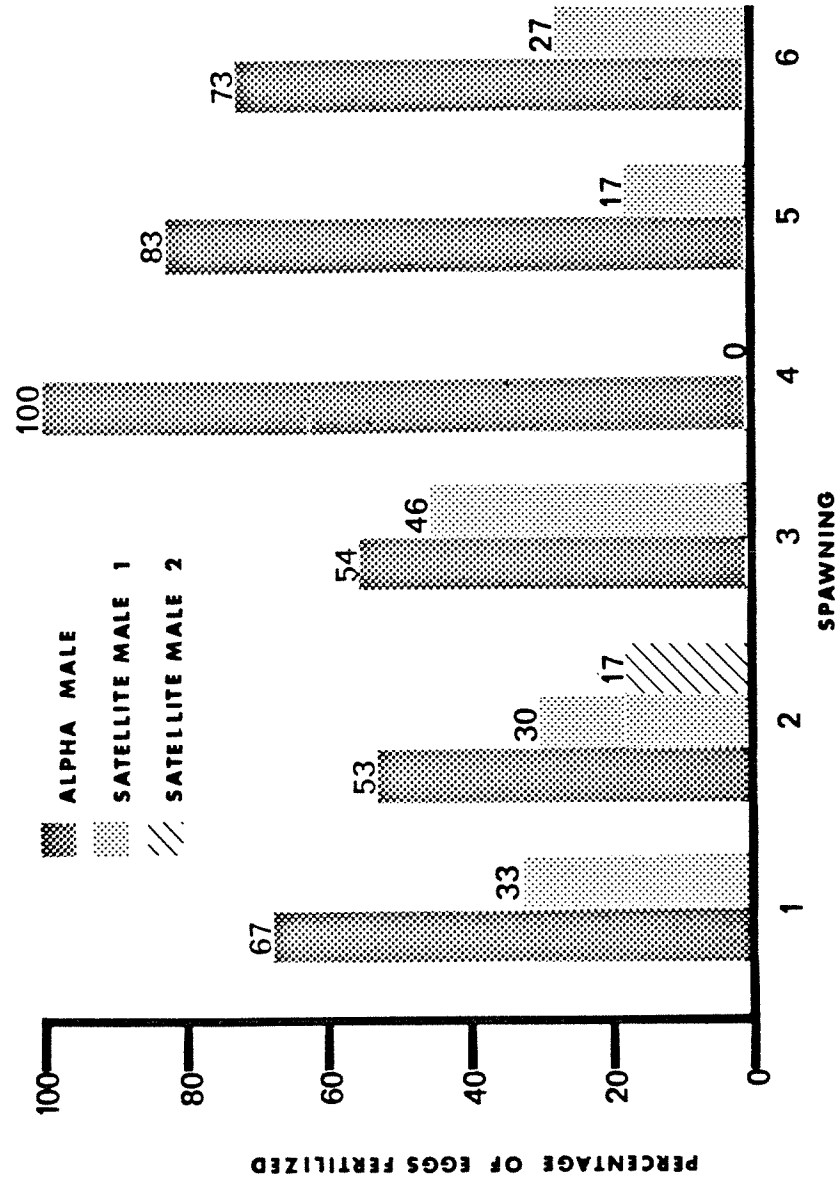


Fig. 13. The estimated gametic contribution of alpha and satellite males during natural spawnings. Each number represents the estimated percentage of eggs fertilized by each male during one spawning act.

ten times. In another case (spawning No. 4, Fig. 13) the satellite male spawned with the pair but did not fertilize any eggs. Apparently, this occurred because during the spawning act he was lying next to the alpha male rather than the female.

One factor that could have affected the data presented in Fig. 13 was the fertility of the males involved in each mating. It is difficult to assess male fertility since it can vary from one day to the next (cf., p. 129). However, I did artificially cross some of the alpha and satellite males with the females they had spawned with. In every instance (Table 9) the males appeared to be equally fertile.

Evidence of Female Choice and Its Effect on the Reproductive Success of Males

The above observations suggest that the potential reproductive success of a male is influenced by his size and strength relative to other males and the OSR existing within his spawning community. In general "large" males appear to have a reproductive advantage over relatively smaller rivals. However, the ability of a male to fertilize eggs may also be affected by female choice.

Current selection theory predicts that the sex making the greatest parental investment will be more selective about who it mates with than the less heavily investing one (Trivers 1972). Chum salmon males do not establish territories nor do they provide parental care. On the other hand, female salmon produce large, nutrient rich eggs, and procure territory locations where they bury and guard their young for several

Table 9. The results of the fertility examinations performed on some of the chum salmon males used to estimate the gametic contributions of satellite and alpha males.

Spawning	No. of eggs in each artificial cross that were examined	Percentage of eggs fertilized		
		Alpha male	Satellite 1	Satellite 2
1	50	100	98	
2	50	76	78	76

days or longer. Consequently, female salmon are expected to exercise more judgement in mate choice than males.

Because chum salmon females cannot discriminate among males on the basis of territory quality, or their willingness to participate in parental care they are forced to choose their mates on the basis of their genetic qualities. They can accomplish this by evaluating how a male behaves (particularly in intramale competition) and by his physical attributes e.g., body size, etc. Obviously, the behavioral and physical traits a female uses when choosing a mate should correlate with her inclusive fitness, be variable, difficult to disguise, and discernible prior to mating (Searcy 1979). The only two traits in male chum salmon that could potentially fulfill all the above criteria are their color patterns and body sizes.

By inspecting the color patterns of the males that court her, a female can conceivably obtain information about their physical condition and social status. For example, as a male remains in freshwater, injuries, pathogenic infestations, and other factors obliterate his normal reproductive appearance. Field observations made on females courted by males in poor physical condition indicated that these fish did not readily spawn, even when they were sequestered from other conspecifics. Two possible explanations for this phenomenon are that such males are not as fertile as newly arriving fish or the elimination of normal body coloration may remove species-specific cues that allow females to "recognize" conspecific males.

The latter speculation appears to be most plausible. The results of the hatchery experiments designed to examine temporal changes in male fertility showed that male chum salmon were able to fertilize eggs up to the time of their deaths (Fig. 14). This is not too surprising since the potential fitness of a male depends to a large extent on the number of eggs he is able to fertilize. Consequently, strong selection pressures have probably been exerted on males to remain fertile for as long as possible. However, periods of infertility did occur. Moreover, they appeared to be associated with the "water content" of the ejaculate. When over 96% of a milt sample consisted of evaporable constituents fertility declined (Fig. 15). Yet, it is apparent from Fig. 14 that the length of time a male remained in freshwater (and thus presumably his physical appearance) was not necessarily linked with the "water content" of his ejaculate.

The above observations make it clear that male fertility is not easily assessed by females and therefore it is probably not a factor in mate choice in this species. Nevertheless, the color pattern of a male may provide a female with important information of another sort. Kees Groot (personal communication) in an ingenious experiment, ascertained that a male's social position relative to other sexual rivals is reflected by his color pattern. Groot placed adult chum salmon into an aquarium and allowed the fish to form pairs complete with satellite males. He noticed that the satellite males and females had the stripe color pattern while the alpha males all possessed the bar pattern. Moreover, he was able to quickly (within seconds) alter the color pattern of an

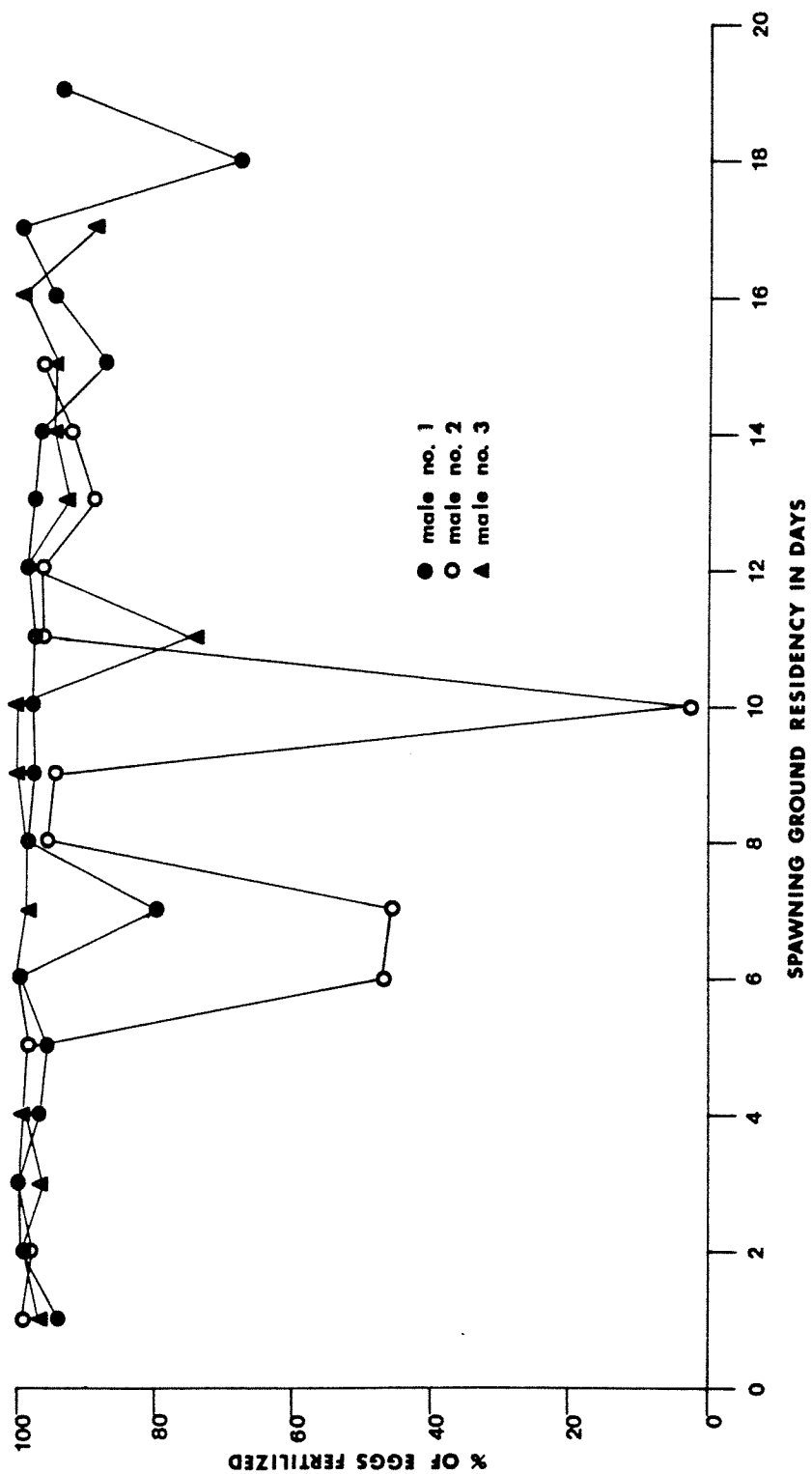


Fig. 14. The effect of freshwater residency on the fertility of three chum salmon males.

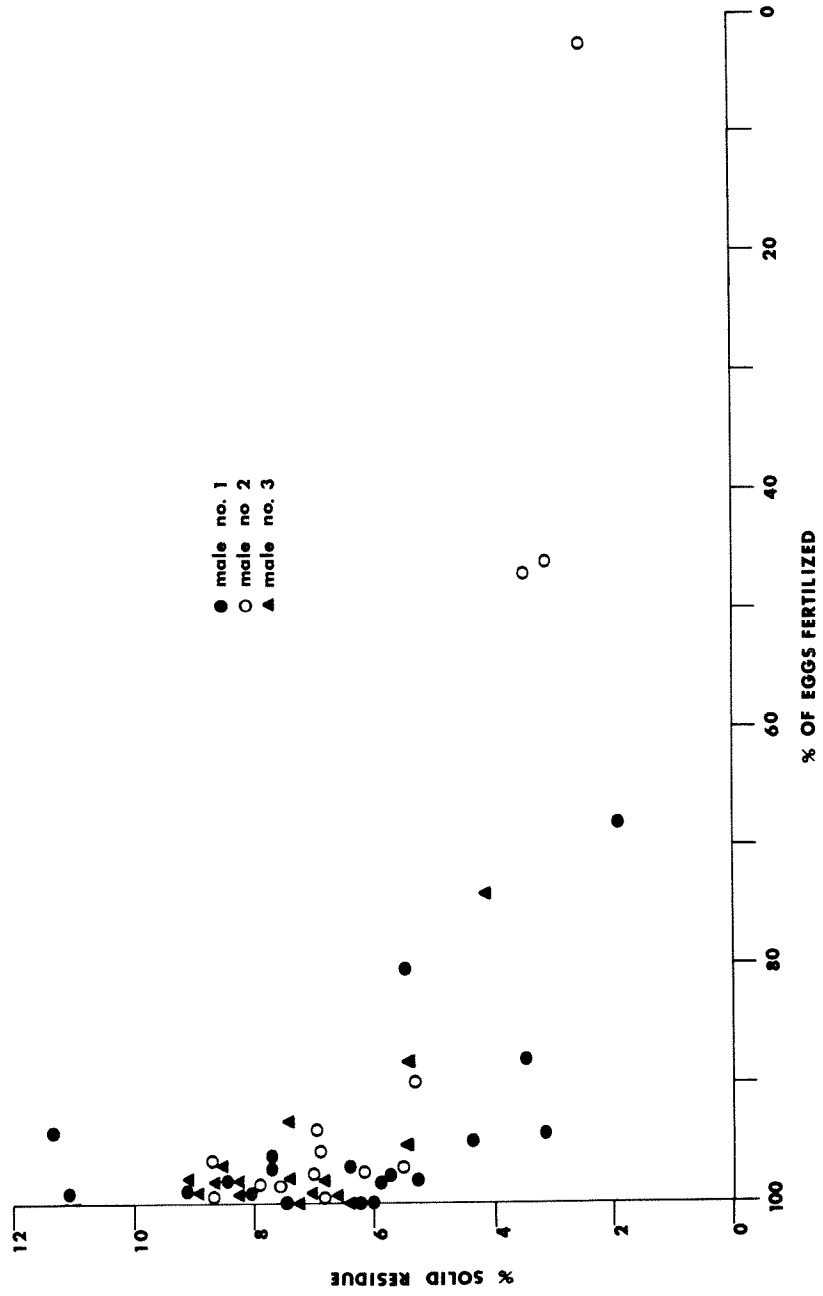


Fig. 15. The relationship between fertility in chum salmon males and percentage of evaporable constituents in their ejaculate.

alpha male by striking its side with a broom handle. Invariably, the struck male lost his vertical bars and developed a dark lateral stripe. Once the broom handle was removed, the alpha male would usually nip at adjacent satellite males and in the process resume the bar color pattern.

Other empirical observations tend to confirm the apparent association between male dominance and the bar color pattern. Groot discovered that he could predict the outcomes of ritualized battles between males by observing their color patterns. At the onset of such contests both males usually possess the bar pattern. However, during the later stages of a confrontation the weaker of the two males always loses this color pattern and develops a lateral stripe.

The observations I made in the experimental stream (Fig. 16) generally corroborate those made by Groot. Although, as Fig. 16 shows, not all alpha males have bars, nor all satellites stripes. If an alpha male was intimidated by a neighboring male he often lost the bar color pattern. Additionally, there was an apparent decrease in the number of alpha males having bars in those sections of the artificial stream where intrasexual competition for females had become intense. This probably occurred because these males were constantly being interrupted or attacked by sexual rivals. The presence of the bar color pattern on wandering males seemed to remain about the same ($\approx 40\%$) within the range of the OSRs examined. This was also true for satellite males who persistently possessed the stripe color pattern ($\approx 96\%$ of the time) except when they

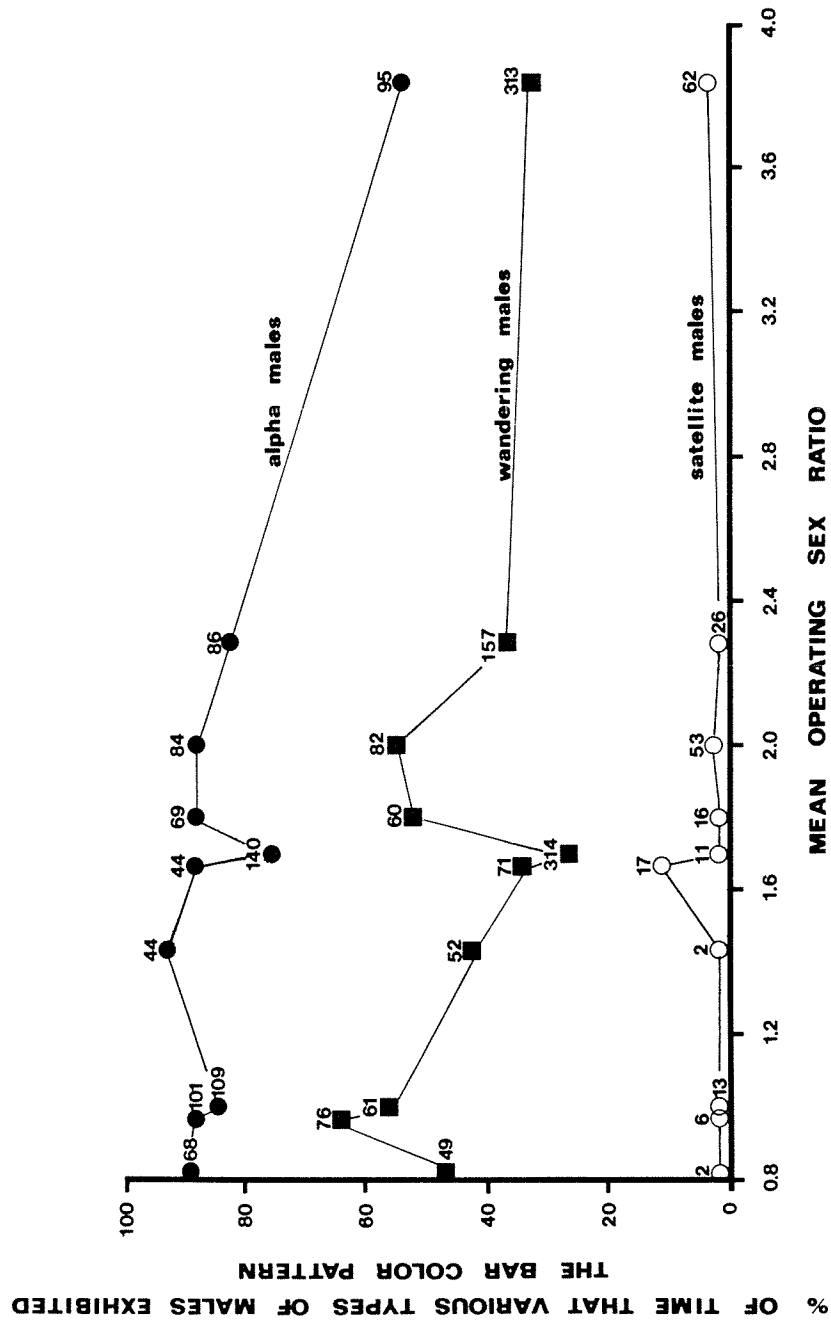


Fig. 16. The occurrence of the bar color pattern on alpha, wandering, and satellite males under a variety of OSRs. The quantity adjacent to each symbol represents the number of males observed in each category.

engaged in ritualized fights among themselves. Female chum salmon also exhibit the bar pattern, particularly in the early stages of their freshwater residency. However, once they begin to construct their first nest they always develop a dark lateral stripe. After this occurs, a female retains this color pattern until she dies.⁷

The above color patterns, and the ability of the fish to rapidly shift from one morph to another are apparently the consequence of two distinct selection pressures. First, it is advantageous for male and female salmon to recognize the sex of other conspecifics and to be able to express their own gender. For instance, Selander (1965) has suggested it pays females to advertise their femininity in species where vigorous intrasexual competition occurs among males, inasmuch as such traits should reduce male aggression during courtship and mating. In chum salmon a decrease in intersexual aggression probably allows females to construct nests and bury their eggs in a more expeditious manner than if they were continually mistaken for males and subsequently attacked. Besides possibly avoiding male aggression, "feminine" appearing females should also attract more potential mates, simply because males can quickly identify them. An increase in "attractiveness" will provide a female with a greater array of males to choose among and thereby enhance her chances of selecting superior mates. Moreover, the amount of time such females will need to deposit their eggs will depend more on their

⁷In an experiment designed to determine whether males preferred "large" or "small" mates (cf., pp. 48, Chapter II) one female developed bars while repeatedly attacking another one. This was the only time, during three field seasons, that I observed a territorial female lose her stripe color pattern. However, the color patterns of females were not as closely observed as those of males and consequently shifts may occasionally occur.

abilities to construct and bury nests rather than on the presence or absence of males. This is an important consideration, since the sooner a female can deposit her eggs, the longer she can protect them from mechanical shock (and presumably death) caused by the digging activities of neighboring fish.

Males that can recognize females should also be favored by natural selection because they will spend less time searching for mates and make fewer fruitless attacks on females. Clearly, male attacks on females are expensive since they deplete the energy stores of the attacking animals and delay females from completing their nests and spawning. Any delay in this procedure increases the likelihood that the attacking individuals will be usurped by more powerful rivals.

Selection pressures are also expected to cause males to develop masculine traits that repulse or threaten rivals or attract females. Additionally, in species where paternal care is nonexistent, males are expected to exaggerate phenotypic attributes that may relate to their genetic quality (Williams 1975, Wilson 1975).

Indeed to the human eye, and most likely to all vertebrate eyes (L. Smith, personal communication), bars that run perpendicular to the long axis of an object tend to magnify its width, while those running parallel to the long axis appear to reduce its bulk. The bar color pattern may thus serve to enhance the apparent width or size of a male. Such deceitful coloration would be favored by natural selection because it pays a male to amplify his size to sexual rivals and potential mates

alike (e.g., see p.11-12, Chapter I). Perhaps too, the ubiquitous stripe on territorial females disguises their size and thereby makes them less threatening to conspecifics.

The above considerations imply why different color patterns may exist on reproducing chum salmon and suggest some possible purposes, besides sex identification, for each color pattern. However, the fact that males rapidly shift their color pattern in concert with their apparent social status requires the identification of another set of selection pressures. Recently, Rohwer et al. (1980) demonstrated that young males in several species of birds have plumage patterns that mimic those of conspecific females. "Female mimicry" has also been observed in insects (Thornhill 1979), hyenas, mountain sheep, salamanders (see Thornhill 1979 for references) and several species of fish (Barlow 1967, Constantz 1975, Dominey 1980, Gross and Charnov, in press). Rohwer et al. (1980, p. 430) hypothesize that such mimicry will occur "...when 1) competition for breeding resources is rigged against [young males or a segment of the male population], 2) when obtaining a mate depends upon holding female-worthy resources, and 3) when females are limiting to males..."

Conditions one and three commonly prevail in chum salmon demes (cf., Table 5, Figs. 8 and 9) and thus the use of the stripe pattern by subordinate males may represent a form of female mimicry. The development of such a reproductive strategy was probably enhanced in this species because these animals can rapidly shift their color patterns.

Consequently, it is possible for the same male to mimic a female in one social situation and "show off" his masculinity under a different set of circumstances. This ability to quickly shift from a "masculine" color morph to a "feminine" one reduces some of the costs a male might accrue if he constantly mimicked females or always displayed his masculinity. An ancillary observation supporting female mimicry in this species is that "small" males, like females, do not possess strongly hooked beaks or large teeth. Such morphological features typically occur on "large" males. Thus, relatively "small" and young males which are commonly subordinate to larger and older individuals are preadapted to resemble females.

Presumably "female mimics" avoid repeated attacks by other males and therefore are able to position themselves next to females. This, in turn, provides them with opportunities to "steal" fertilizations from sexual rivals or in some circumstances to surreptitiously court females. The cost of such a strategy lies in the reluctance that females should exhibit to such suitors.

Alternatively, the stripe pattern may function as an appeasement stimulus (Stacey and Chiszar 1978). The genetic maintenance of such a behavioral signal could occur because it does not pay a male to continuously attack a clearly subordinate opponent. Such attacks would drain the limited energy reserves of a male and could also lead him away from females he is attempting to court. In a promiscuous species like chum salmon, a short absence from an "active" female could cost an overly

aggressive male a considerable number of fertilizations.⁸ Clearly, too, the ability to communicate subordination is also beneficial in that it allows a male to escape repeated attacks by stronger rivals.

However, if the stripe pattern is an appeasement stimulus it has to be a sex-specific one. Plainly territorial females should regard individuals with stripes (presumably other females) as potential threats to their buried eggs or as possible competitors for space. In fact, 80 to 90% of the agonistic interactions that occur around courting pairs are intrasexual. When males are attacked by females they usually possess the stripe pattern.

Attacks by females can be prolonged or repetitious and are probably bothersome to males. Consequently it is unlikely that males develop the stripe pattern solely to avoid aggression. This speculation is further buttressed by the fact that males often possess this color pattern even when they are not being attacked or threatened. Whatever the ultimate causations of the stripe and bar patterns, they nevertheless convey information of interest to females.

Current theory (cf., p.11-13 , Chapter I) predicts that females may

⁸This was dramatically illustrated by an incident that occurred in the experimental stream. A fairly aggressive male attacked and then chased a sexual rival away from the female he was courting. During his brief absence the female finished her nest and then adopted the open-mouth posture that signified that she was ready to spawn. An upstream male that was courting another female noticed her display. He quickly swam downstream, spawned with the female, and then returned to the upstream female. Meanwhile, when the original male returned from his aggressive foray ($\approx$ 40 sec later) the female he had been courting was rapidly burying her eggs!

prefer mates that have high social status or relatively large size. As we have seen, the bar pattern clearly connotes social dominance among males. Furthermore, as Fig. 17 illustrates, it often indicates the relative size of a male as well, for plainly "large" males generally dominate smaller ones. Thus, females should prefer to mate with individuals having bars. Data collected from the videotapes were used to test this prediction and to determine if a male's absolute size also affected female behavior.

Female Expression of Mate Choice I: Tardiness in Nest Construction.

One of the easiest and most energetically conservative ways a female can "select" who spawns with her is to delay or accelerate her nest construction activities. For example, by slowing down nest construction a female increases the likelihood that additional males will discover her. Consequently, a male courting such a female will most likely be forced to defend his position against newly arriving rivals. In this parsimonious fashion the female is able to "choose" the most aggressive and probably largest male in her vicinity. On the other hand, it also pays a female to deposit her eggs as quickly as possible. Thus, if a female is courted by a male exhibiting high social status (i.e., one with bars) or large body size, she may attempt to construct her nests as rapidly as possible.

A straightforward way to quantify the existence of such a feminine tactic is to measure the amount of time females spend on nest construction while being courted by males with different color patterns and body

sizes. In Table 10 the length of time it took female chum salmon with various types of sexual partners to complete their first two attempts is summarized. The coefficient of variation (C.V. - Sokal and Rohlf 1969) data presented in the table show that fluctuations in the time required to complete a nest were greatest when the male possessed the stripe color pattern or was one-half the size of the female. The C.V. values also tended to diminish (by 90%) from the first to the second nest. I believe that this variation reflected the "physiological condition" of the females, i.e., those that were quickly regarded as "undesirable" (those that were quickly regarded as "undesirable" was courting them) and their reluctance to spawn with their male partner.

Statistical analyses were performed only on complete second nests in order to standardize the physiological condition of the females. These analyses, Mann-Whitney U Test of the effect of color patterns and a Kruskal-Wallis one-way ANOVA on the influence of male size, revealed that females took less time to complete their second nests when they were courted by males with bars ($U = 20, p = 0.001$, $n_1 = 11, n_2 = 61$) or by males of their own size or larger ($U = 5.47, p = 0.05, 2 \text{ but } > 4.67 \times^2 .10, 2$).

Correlation analyses were also performed on these data to ascertain whether water temperature influenced the results of the analyses. The results of the correlation analyses showed that the partner was held constant within each correlation since these factors appeared to have influenced female behavior. The results of these tests

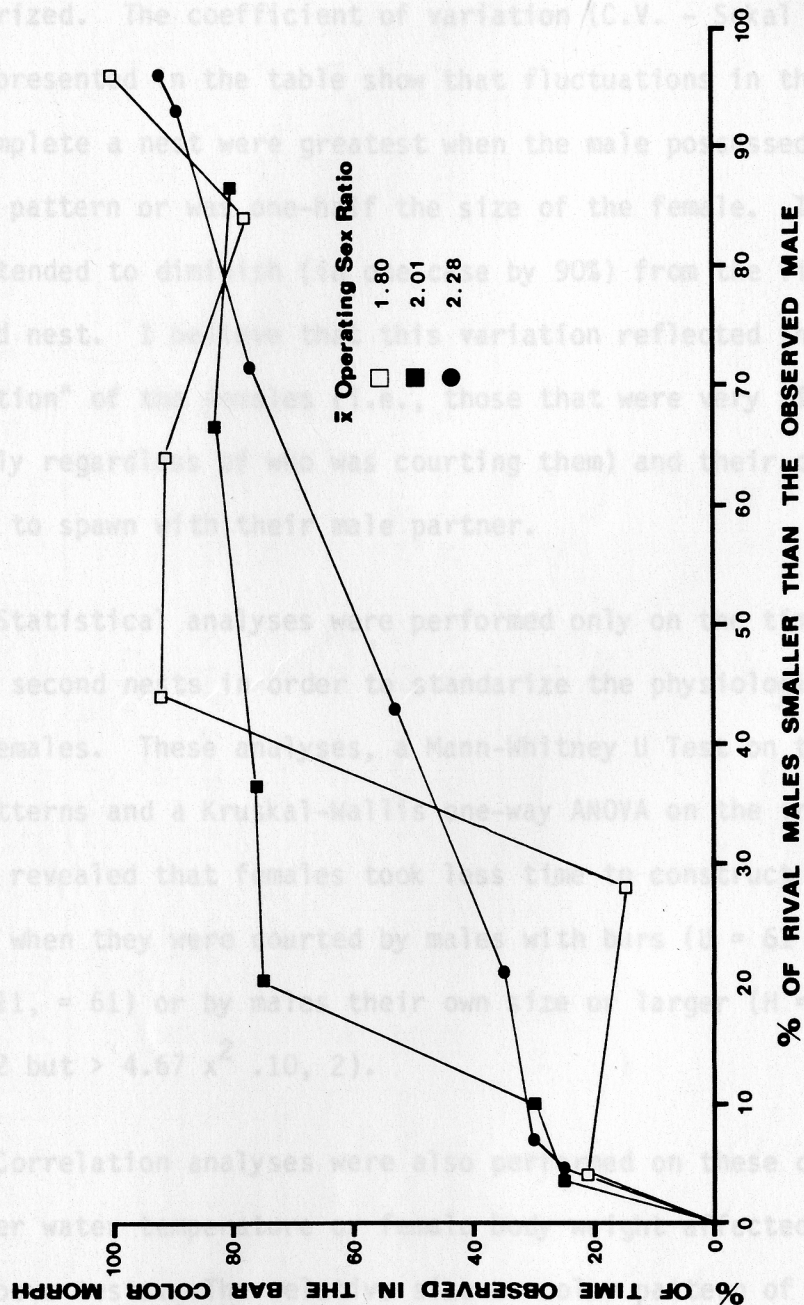


Fig. 17. The association between body size and the occurrence of the bar color pattern in spawning chum salmon males.

sizes. In Table 10 the length of time it took female chum salmon with various types of sexual partners to complete their first two nests is summarized. The coefficient of variation (C.V. - Sokal and Rohlf 1969) data presented in the table show that fluctuations in the time required to complete a nest were greatest when the male possessed the stripe color pattern or was one-half the size of the female. The C.V. values also tended to diminish (in one case by 90%) from the first to the second nest. I believe that this variation reflected the "physiological condition" of the females (i.e., those that were very ripe spawned quickly regardless of who was courting them) and their desire or reluctance to spawn with their male partner.

Statistical analyses were performed only on the time needed to complete second nests in order to standardize the physiological condition of the females. These analyses, a Mann-Whitney U Test on the effect of color patterns and a Kruskal-Wallis one-way ANOVA on the influence of male size, revealed that females took less time to construct their second nests when they were courted by males with bars ($U = 61 \geq U .05, n_1 = 7, n_2 = 11, = 61$) or by males their own size or larger ($H = 5.47 < 5.99 \chi^2 .05, 2$ but $> 4.67 \chi^2 .10, 2$).

Correlation analyses were also performed on these data to ascertain whether water temperature or female body weight affected the results of the above tests. The relative size or color pattern of the male partner was held constant within each correlation since these factors appeared to have influenced female behavior. The results of these tests

Table 10. The time needed by female chum salmon to complete their first and second nests while being courted by variously sized or colored conspecific males.

Type of sexual partner	First nests					Second nests				
	N	$\bar{x}$ time (min)	S^2	C.V.* %	Range	N	$\bar{x}$ time (min)	S^2	C.V.* %	Range
♂ body wt<♀ body wt	9	240.6	64583.3	105.64	84-874	9	170.00	2665.3	30.37	115-261
♂ and ♀ with=equal body wts	8	129.1	2812.7	41.07	74-210	6	123.5	149.5	9.90	100-133
♂ body wt>♀ body wt	6	107.2	603.8	22.92	74-136	5	140.4	1151.3	24.17	112-170
♂ with stripe color pattern	10	203.0	63037.8	123.68	74-874	11	163.5	2283.3	29.23	112-261
♂ with bar color pattern	10	137.6	2057.2	32.97	74-210	7	119.7	112.9	8.88	100-133

*C.V. = Coefficient of variation = $(S)(100)/\bar{x}$.

(Table 11) clearly showed that neither water temperature nor body size affected how rapidly a female constructed her first two nests.

Thus, I think it is safe to conclude that females delay nest construction while being courted by socially subdominant or relatively small males. One may wonder if the time differences shown in Table 10 increase the likelihood that courting males which are relatively small or subdominant-appearing will be evicted by sexual rivals. In many chum salmon demes heavy concentrations of spawners may commonly occur (e.g., in short coastal streams). Under these social conditions a 1- or 2-hr delay would certainly allow additional males to discover an "active" female. Moreover, it should also be remembered that while the pairs were being filmed they were not interrupted by neighboring fish and hence the data represent the minimum amount of time a female would spend in developing a nest.

Female Expression of Mate Choice II: Changes in the Frequency or Performance of Reproductive Behavior. Cox and LeBoeuf (1977) have hypothesized that certain postures or locomotor activities performed by females serve to signal their sexual receptivity and also provoke intramale competition. These activities are referred to as incitation movements since they induce intrasexual competition among members of the limited sex (i.e., the sex making the smallest parental investment). I believe that most of the behaviors performed by female chum salmon while they construct and test their nests simultaneously act as incitation movements. Females are to a large extent locked into a small portion of the

Table 11. The effects of water temperature and female body weight on the amount of time needed to construct nests.

Type of correlation	Range of water temperature (C)	D.F. (N-2)	r	Conclusion ($\alpha .05$)*
Water temperature vs time needed to complete the first nest when the male partner:				
a) weighed 1/2 as much as the $\bar{q}$	3.9-12.2	7	-.296	fail to reject H_0
b) weighed approximately the same amount as the $\bar{q}$	7.5-12.7	4	-.270	"
c) weighed at least twice as much as the $\bar{q}$	5.3-11.8	4	.075	"
d) possessed the stripe color pattern	5.3-10.9	8	.026	"
e) possessed the bar color pattern	3.9-12.2	8	-.358	"
Water temperature vs time needed to complete the second nest when the male partner:				
a) weighed 1/2 as much as the $\bar{q}$	3.9-12.2	6	-.706	fail to reject H_0
b) weighed approximately the same amount as the $\bar{q}$	7.5-12.7	4	-.049	"
c) weighed at least twice as much as the $\bar{q}$	5.3-11.8	3	.330	"
d) possessed the stripe color pattern	3.9-11.8	8	-.257	"
e) possessed the bar color pattern	8.2-12.2	5	-.390	"
Female body weight vs time needed to complete the first nest when the male partner:				
a) weighed 1/2 as much as the $\bar{q}$	3.7-5.8	7	.310	fail to reject H_0
b) weighed approximately the same amount as the $\bar{q}$	2.6-4.8	6	.060	"
c) weighed at least twice as much as the $\bar{q}$	1.9-3.3	4	.570	"
d) possessed the stripe color pattern	1.9-5.8	8	.440	"
e) possessed the bar color pattern	2.6-5.5	8	.320	"
Female body weight vs time needed to complete the second nest when the male partner:				
a) weighed 1/2 as much as the $\bar{q}$	3.7-5.8	7	.740	reject H_0
b) weighed approximately the same amount as the $\bar{q}$	2.6-4.8	4	.310	fail to reject H_0
c) weighed at least twice as much as the $\bar{q}$	1.9-3.3	3	-.460	"
d) possessed the stripe color pattern	1.9-5.8	8	.510	"
e) possessed the bar color pattern	2.6-4.8	5	.430	"

*A significant negative slope would indicate that either warm water temperatures or large body size accelerated nest development.

streambed and thus the most economical way for them to advertise their sexual status and attract suitors is through their nest construction activities. Since these movements are intimately associated with egg deposition, males are expected to be highly attuned to them.

Conceivably, then, females that are courted by males of apparently "poor quality" (i.e., by "small" or subdominant individuals) could increase the frequency of some of their behaviors in an attempt to attract additional males and precipitate male x male interactions. Ethograms produced from the videotape films made in the viewing chamber were analyzed to determine the total number of times females performed a variety of locomotor activities while they constructed their nests. The square root transformation was used on these data and the resulting random variables were tested for normality. An assortment of statistical procedures were then employed to determine if the relative size or color pattern of the courting males influenced the occurrence of any of these activities.

Tautz and Groot (1975) discovered that chum salmon females perform different activities as their nests develop. Intuitively, one would expect that those activities emerging as a nest nears completion would be more powerful attractants than those which typically occur at the beginning of nest construction. Therefore, some of the statistical analyses were devoted to analyzing the events that occurred within the last hour of nest construction. Moreover, certain feminine behaviors such as digging, weaving, etc. (definitions for these terms are provided below) can potentially broadcast the location of a female via acoustical,

visual, or olfactory cues. Hence, the frequency of these activities was also examined.

Behavioral activities performed by breeding chum salmon. After introduction into the viewing chamber each female quickly explored the structure and then often remained quiescent for 30 to 40 min. Just prior to searching for her first nest site a female invariably broke the surface of the water with her beak and "gulped air." She then lowered her head and released air while descending slowly to the substrate. Such air-gulping was often repeated for 3 to 4 min before the fish began "nosing" the substrate. During a nosing episode the head was pointed toward the substrate (often in contact with it) while the rest of the body was elevated at a 7 to 15° angle. The pectoral fins were usually fully extended and the female often moved her head from side to side as she slowly progressed upstream. After a nosing bout the fish usually swam back and "dug" into the substrate that she had just passed over. Nosing usually occurred at the onset of each new nest and sometimes was performed well into nest construction.

There are at least five (and possibly as many as seven) different kinds of digging motions, all of which consist of a rapid series of body flexures performed while the female is turned on her left or right side. During each dig the pectoral fins are held at a 90° angle from the body

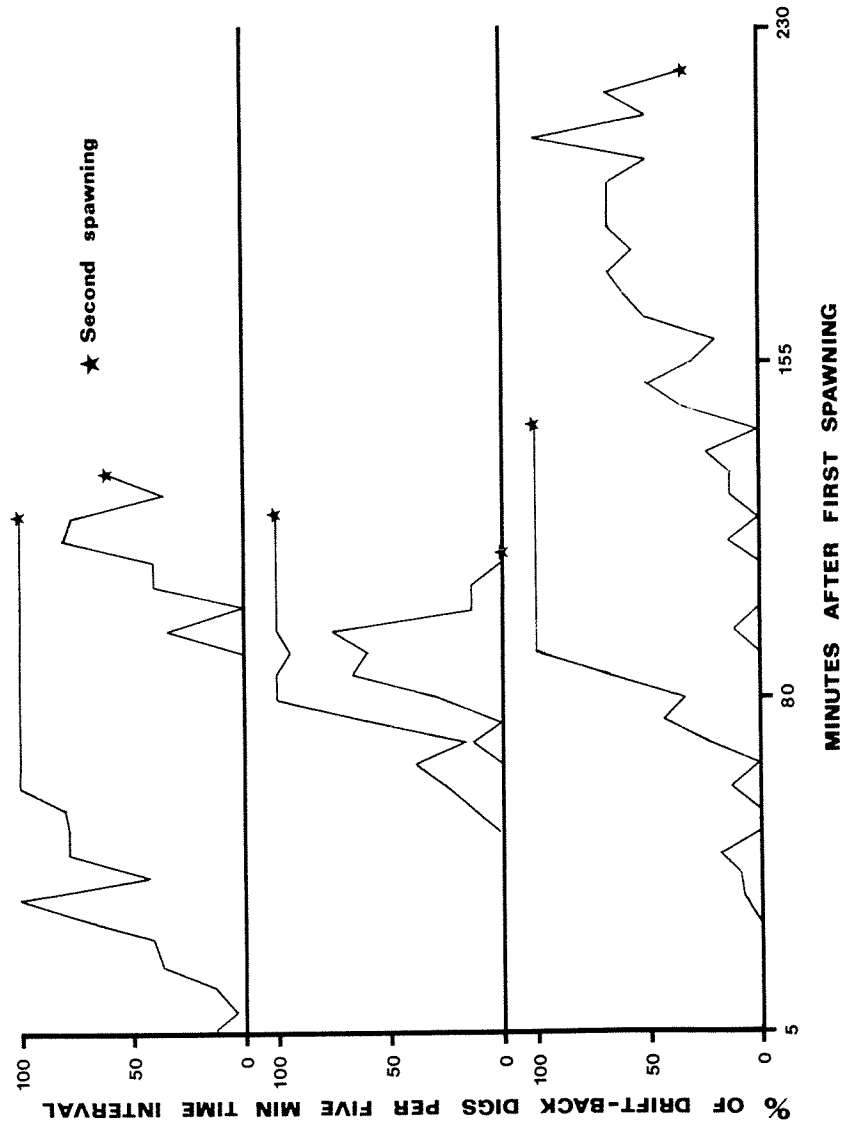


Fig. 18. Temporal changes in the occurrence of drift-back digging movements performed by six females while they constructed their second nests. Each point represents the percentage of drift-back digging movements a female made over a 5 min time period.

wall and appear to function as brakes.⁹ Prior to establishing a territory, females may "nose" and dig ("exploratory digging") over a fairly large area. However, once a suitable nest site has been found, their digging movements ("nest digging") become concentrated into a smaller and smaller area (Tautz and Groot 1975). Normally after each dig the females turn (either to the left or right) and leisurely swim back to their developing nests. These turning and subsequent circling motions probably provide females with opportunities to visually inspect their nests (Duker 1977), detect any invasions by adjacent females, and possibly observe the phenotypic traits of their prospective mates. As a nest nears completion the tendency for females to turn and circle after each dig commonly decreased (Fig. 18). Instead they often let the current push them, tail first, back into their nest depression ("drift-back" digging).

Perhaps the most conspicuous digging takes place 15 to 30 min after spawning. Within seconds after egg deposition the female moves upstream and gently flexes her body once or twice. These "covering" movements are performed almost as rapidly as the female can return to her nest, and become more vigorous as the nest pocket fills with gravel. Every

⁹Sometimes the mouth is slightly agape and this likewise tends to hold the female in one place while she performs a digging motion. Male chum salmon also dig, but do so only sporadically and never help in nest construction. Moreover, unlike females they do not extend their pectoral fins (Groot, personal communication) while digging and thus tend to "skip" along the substrate surface rather than "cut" into it. McCart (1969) feels that male digging is a displacement behavior, inasmuch as it commonly occurs after a male has been thwarted by a sexual rival.

covering dig is either performed slightly upstream or to one side of the nest. Apparently, this expedites the burial process, prevents the eggs from being dislodged, and also maintains the morphological integrity of the nest.

The purpose of the initial gentle covering motions became apparent once the structural features of nests and the egg burial process were observed from the bottom window of the viewing chamber. Generally, nests are shaped like cones, with the base located at the substrate surface and the tip about 20 to 40 cm below the surrounding gravel bed. In the process of digging their nests, females create a porous layer of gravel around the bottom portion of the nest. The first few "covering" digs tend to drive the eggs down and into this gravel labyrinth (Tautz and Groot 1975). Moreover, the water surges created by these motions purge the nest of excess sperm, blood clots, and ovarian fluid.

Once a female has completed all of her nests she will usually attempt to bury them under a single mound of gravel. To accomplish this, prolonged and curving digging motions are performed that commonly consist of 15 to 20 body flexures (Groot, personal communication). Such "post-spawn digging" activities are easily recognized because covering, nest digging (including drift-back digs) and exploratory digging incorporate fewer body flexures/dig (see Fig. 20, p.) and occur on a more regular basis (see Fig. 19, p.).

Gravel displaced by any of the above digging activities produces a very conspicuous and characteristic sound that can override most back-

ground noises in a stream (I commonly heard "digging noises" while standing 10 m or more away from the experimental stream). Beyond providing acoustical cues, the actual digging act plus any related turning and circling motions provide striking visual cues as well. Consequently, females courted by seemingly "inferior" males could increase or misdirect their digging motions in an effort to attract additional suitors.

This possibility was tested by using Model I two-way ANOVAs. The random variables in these analyses were the number of digs required to complete a nest while the fixed treatments were the relative size or color pattern of the male partner and the nest number (i.e., whether it was the first, second, or third nest).

Besides turning and circling after most of their digging acts, females also commonly swim in tight circles or in a figure-eight pattern over their nests. These locomotor activities are collectively referred to as weaving (after Groot, personal communication). Like the turning motions associated with nest digging, weaving potentially broadcasts the location of a female and indicates that she is sexually active. "Spent" females do not "weave" and except for post-spawn digging and aggressive forays, remain motionless over their redds. Thus, the occurrence of weaving bouts and circling motions after digging were quantified and Mann-Whitney U tests were used to ascertain whether these activities increased or remained the same when females were courted by different types of males.

Like weaving, "yawning" (a prolonged opening of the beak), "spitting" (a quick snapping of the jaws and expulsion of water that usually follows yawning) and "air gulping" are probably "comfort movements."¹⁰ Presumably, females that are courted by socially subdominant or relatively small males may perform more of these activities (if indeed they are comfort movements) than those having more desirable suitors. Accordingly, the number of times these behaviors occurred while the second nest was under construction was determined. These values became the random variables in two Model I two-way ANOVAs. Once again, one of the fixed treatments was the relative size of the male partner or his color pattern while the other main factor was the sex of the fish performing the comfort movement.

Another way that courting fish can potentially express their unease is to attack their prospective mates. Aggression within most pairs rarely occurs (Schroder 1973) but certainly females could exhibit a decided nonpreference by nipping, chasing, or biting a male in an effort to drive him away. ANOVAs similar to those performed above were used to determine whether certain types of pairs experienced more internal aggression than other male-female combinations.

¹⁰Baerends and Baerends von Roon (1950, p. 28) define a comfort movement or behavior as any activity that removes a physiological or psychological discomfort. That is, "...before the movement is carried out the animal is restless, but after it, it looks as if it is more comfortable."

After a nest develops a centralized depression, the female repeatedly lowers her tail and midbody into it and "probes" the substrate with an erect anal fin. Once the anal fin makes contact, the female usually bounces back to her original horizontal position. She may then weave, dig, etc., or perform another probe. As the nest develops, the angle that the body has to assume during a probe becomes more and more pronounced until it reaches approximately 20° (Tautz and Groot 1975). At this time the nest is complete. Generally probing increases as a nest nears completion but decreases slightly just before spawning commences (see Fig. 19, pp. 154-157; Tautz and Groot 1975).

Just prior to spawning a female will often open her beak and gape while making a probe. This conspicuous display exposes the predominantly white inner mouth coloration of the female. "Crouching" is almost an identical open-beaked posture except that the female remains pressed against the substrate rather than quickly rocking back to a horizontal posture. If a male is present when a crouch is performed, he immediately lies next to the female and assumes a similar posture. In most cases spawning will then transpire. However, in about a third of the pairs filmed, the females adopted the crouching posture several times (in one case 14 times in 18 min) before spawning finally occurred. Such prolonged displays often caused their male partner to ejaculate milt.

Heard (1972) called such incidences "false spawnings," while Jones and Ball (1954) have referred to them as "false orgasms." Unlike normal spawnings that take approximately 10 secs ($\bar{x} = 9.3$, $s^2 = 5.98$, $n = 44$)

to complete, false spawnings usually last half as long ($\bar{x} = 5.4$, $s^2 = 11.15$, $n = 30$). By delaying egg deposition in this manner a female potentially produces one of the most powerful "incitation movements" in her behavioral arsenal. Not only does this display provide a visual cue that the female intends to spawn in the immediate future, but by inducing the male to release milt it also causes an olfactory one to be broadcast downstream. Newcombe and Hartman (1973) provide evidence that salmonids probably respond to such cues as they found that male steelhead were strongly attracted to the odors of sexual products in a two-choice maze.

Throughout the last hour that the second nests were under construction, I counted the total number of probes and false spawnings that occurred. "T" tests were performed on some of these data to determine whether the size or color pattern of the male influenced the number of probes performed during this period. Additionally, Fisher's Exact Probability Tests with Tocher's modification (Siegel 1956) were employed to ascertain if the phenotype of the male partner influenced the appearance of prolonged crouches or false spawnings.

In Fig. 19, the temporal relationships and frequencies of most of the above female activities are documented on a minute-by-minute basis. Each point on the graphs represents the average number of times an event occurred/min over a 5-min time span. The behavioral responses of the male partner to these female activities are also illustrated.

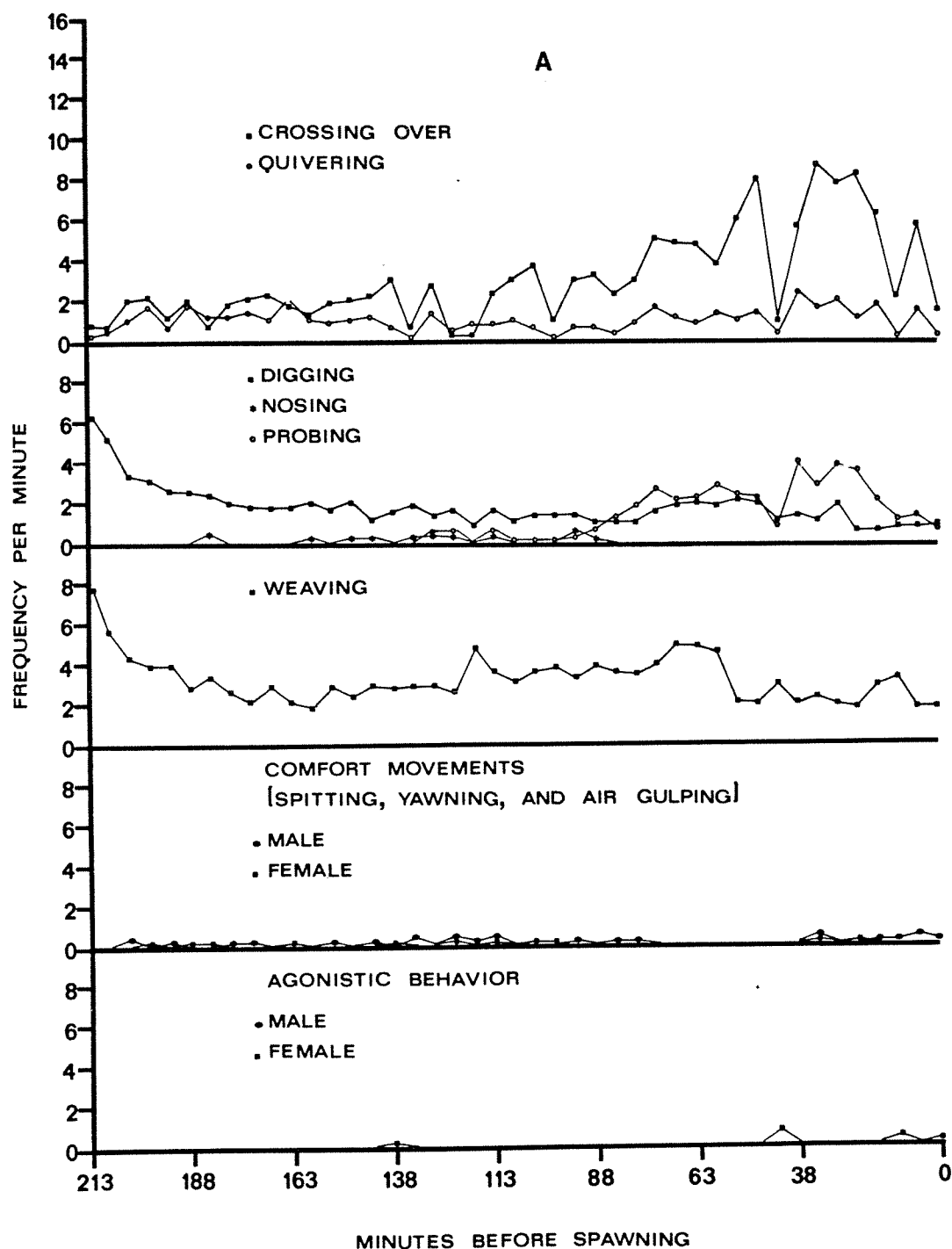


Fig. 19. The temporal relationships and frequencies of the most common reproductive behaviors performed by chum salmon. In part "A" the male was smaller than the female and had the stripe color pattern. The males weighed the same amount as their female partners in parts "B" and "C," although the male in part "B" had a stripe while the one in "C" possessed bars. In part "D" the male weighed more than the female and had the bar color pattern.

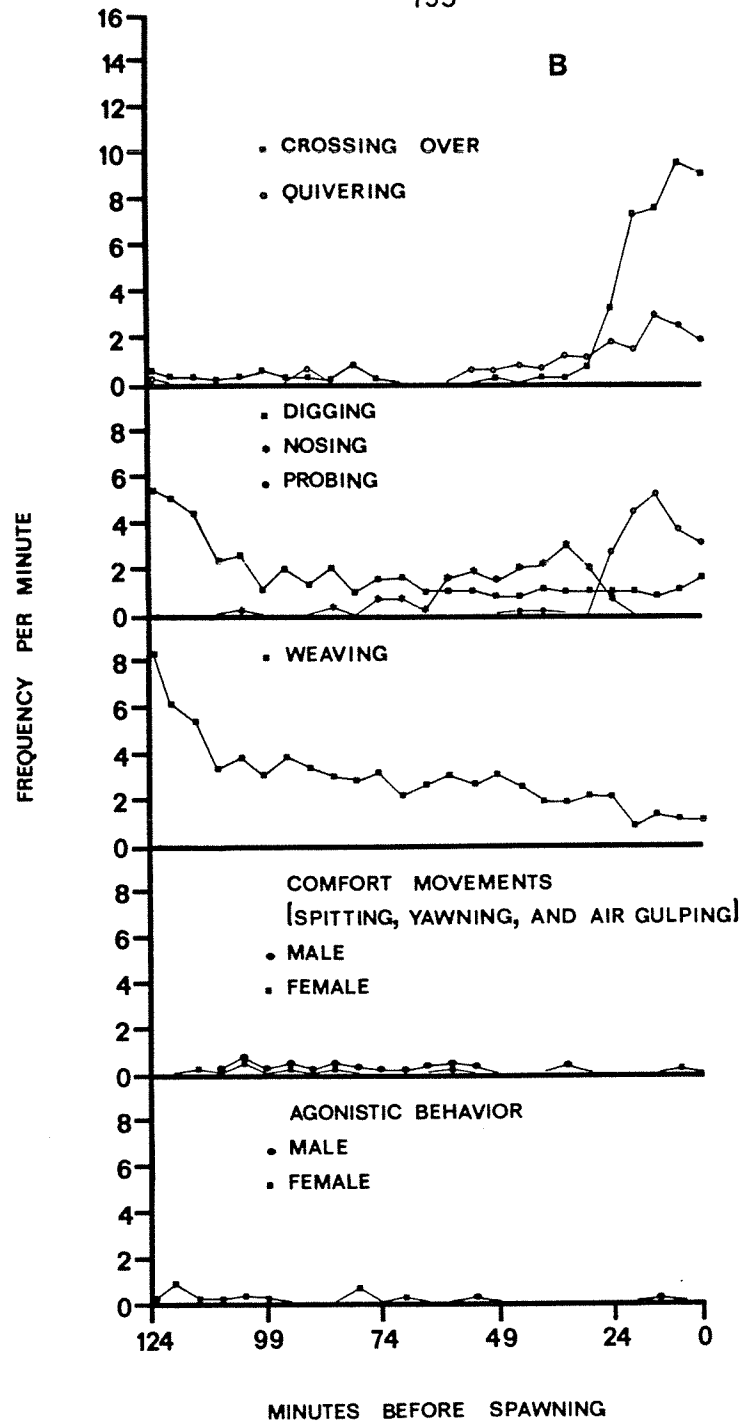


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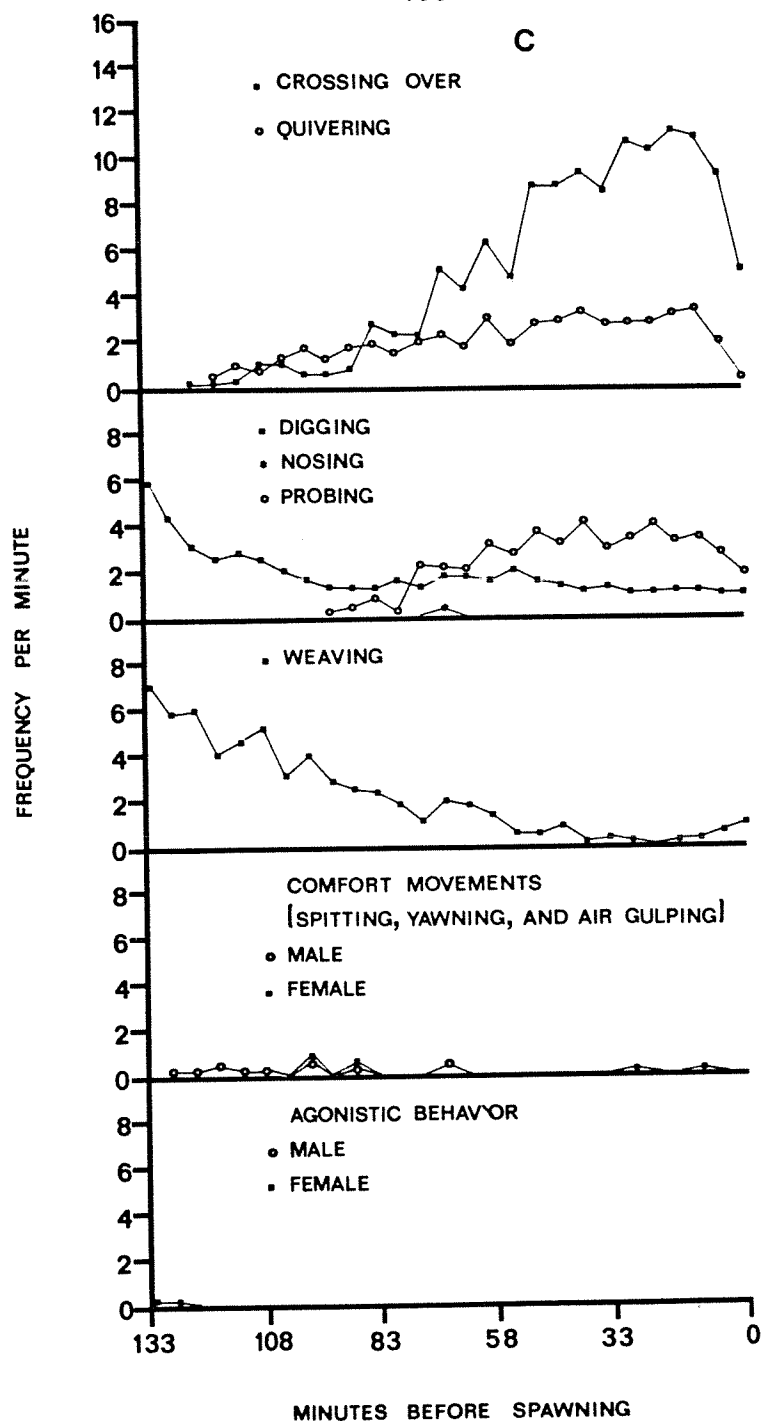


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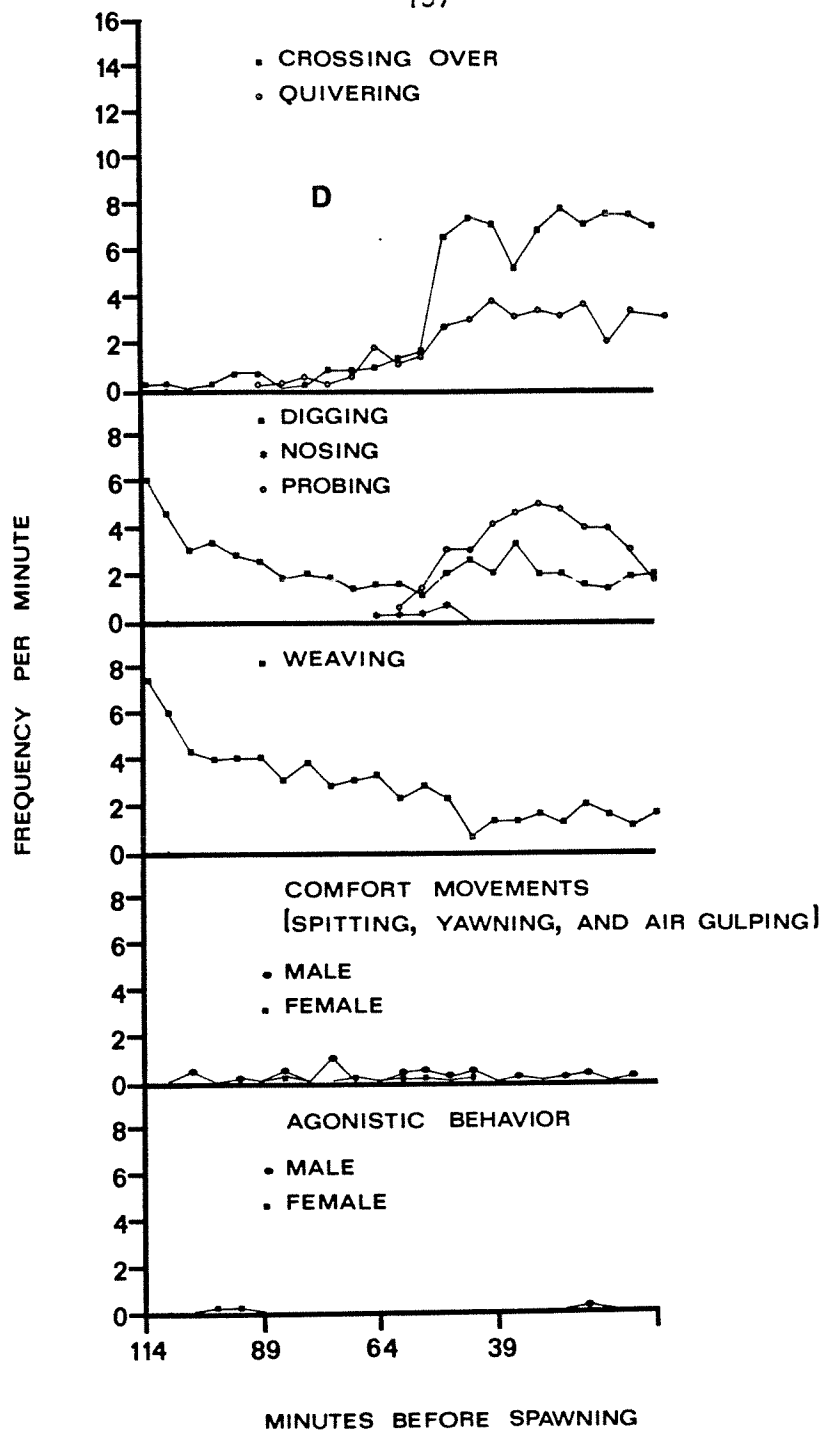


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In general, the principal courtship behaviors of males consist of "crossing over" (the rapid swimming of the male across the caudal peduncle or back of the female) and "quivering" (a darting movement toward the female accompanied by a short and very rapid shaking of the head and body). Crossing-over movements allow a male to continuously inspect both sides of a female and thus presumably detect and evict rivals. Therefore, it is not too surprising that this activity increases as a female approaches spawning (see Fig. 19, Parts a-d). Moreover, this continual back-and-forth motion permits a male to display his color pattern or presence to nearby rivals. It is possible (but as of yet unproven) that the black-red-black placement of bars on dominant males may serve as warning colors to adjacent opponents. However, as the graphs in Fig. 19 show, males possessing a stripe, cross over as often as those with bars. Quivering, on the other hand, seems to serve as an unambiguous sex identifier (only males quiver)--an important function in a species where males can take on seemingly feminine characteristics. In fact, the first "courting movement" a male performs after locating a female is often a quiver. Like crossing over, quivering increases in frequency as a nest nears completion and almost invariably occurs during or immediately after a female probes (Tautz and Groot 1975). Males also spit, yawn, gulp and release air, crouch, and dig (see footnote 9, p. 148), although the latter behavior was never observed in the viewing chamber.

Males quickly respond to certain female movements or postures (Fig. 19). A good example of this can be seen in part "a" where both

crossing over and quivering are greatly reduced (≈ 40 min before spawning) due presumably to a decrease in probing by the female. Nosing also tends to precipitate male attention (see particularly part "b", ≈ 55 min before spawning and thereafter) but not as strongly as probing. Apparently, any behavioral act that causes the female to angle her body toward the substrate, either head or tail first, is an important stimulus because of its probable association with egg deposition.

The influence of male phenotypes on the behavior of sexually active females. Conversely, females were generally not as strongly influenced by their sexual partners. Data analyses showed that the phenotype of the male partner did not noticeably alter the frequencies or the performance of behaviors directly associated with nest construction, i.e., nosing, digging, and probing (Table 12, Fig. 20). Correlations between female body weight and the total number of digging bouts needed to complete a nest indicated that female size also did not influence digging frequencies (e.g., $r = .20$, $v = 18$ for nest one; $r = .25$, $v = 18$ for nest two; and $r = -.32$, $v = 7$ for nest three; all are nonsignificant). However, the number of digs required to complete the first nest was about 50% of that needed for the second and third nests (Table 13; also see Tautz and Groot 1975). This occurred because a considerable number of covering digs were performed before the second or third nest were actually begun. In general, the number of digs required to complete a nest appeared to become more numerous from one nest to the next (e.g., see Table 11).

Table 12. Results of tests performed to determine whether nest construction activities increased or decreased because of the phenotype of the male partner.

Null hypotheses	Random* variable	Type of analysis	No. of pairs examined	Decision
1) The total number of nosing bouts performed while the second nest was under construction remained the same regardless of: a) the color pattern of the male** b) the relative size of the male***	Total no. of nosing bouts	"t"-test	a = 7 b = 7	a - fail to reject H_0 $t = 2.07 < t_{.05(2)5} = 2.571$ b - fail to reject H_0 $t = 0.40 < t_{.05(2)5} = 2.571$
2) The total number of probes performed while the second nest was under construction remained the same regardless of: a) the color pattern of the male** b) the relative size of the male***	Total no. of probes	"t"-test	a = 7 b = 7	a - fail to reject H_0 $t = 0.31 < t_{.05(2)5} = 2.571$ b - fail to reject H_0 $t = 0.84 < t_{.05(2)5} = 2.571$
3A) Neither a) the male color pattern nor b) the relative size***of the male partner influenced the number of digging bouts needed to complete the first or second nest.	Total no. of digging bouts	Model I two-way ANOVAS	a = 30 b = 30	a - fail to reject H_0 $F = 0.11 < F_{.05(2)1,24} = 5.72$ b - fail to reject H_0 $F = 0.90 < F_{.05(2)2,24} = 4.32$
3B) There is no interaction between: a) male color pattern and nest number on the number of digs needed to complete a nest, or b) the relative size of the male**** and the number of digs needed to complete a nest.	Total no. of digging bouts	Model I two-way ANOVAS	a = 30 b = 30	a - fail to reject H_0 $F = 2.32 < F_{.05(2)1,24} = 5.72$ b - fail to reject H_0 $F = 2.18 < F_{.05(2)2,24} = 4.32$

*Square root transformation was used on raw count data.

**Males had either the bar or stripe pattern.

***In these analyses the males either weighed more or less than the female.

****In these analyses the males weighed less than, = the same, or more than the female.

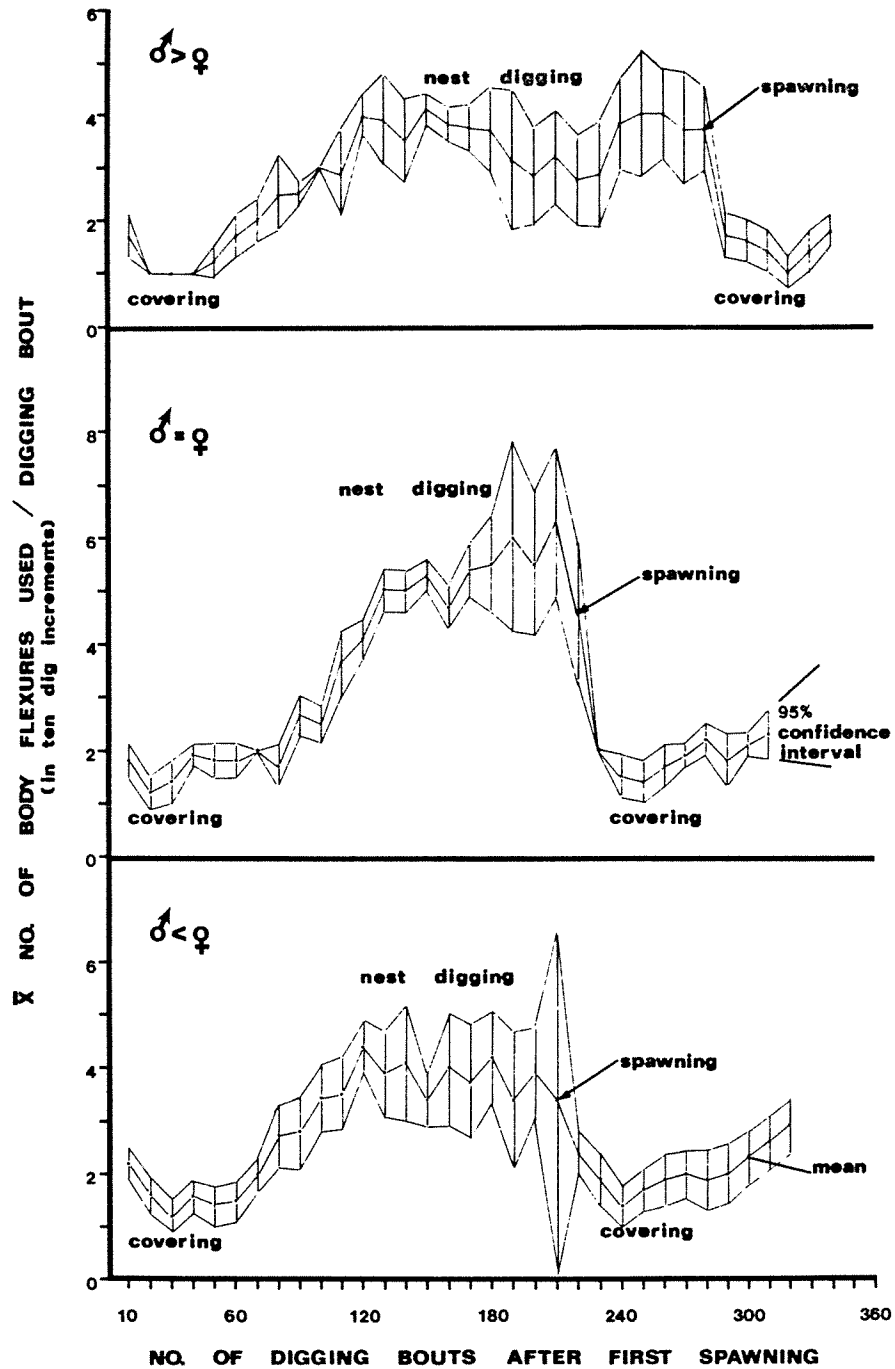


Fig. 20. Temporal changes in the mean number of body flexures used per digging episode before and after spawning by three females that were courted by different types of male partners.

Table 13. Raw data and results of analyses used to determine whether the number of digging bouts needed to complete a nest varied because of female size or nest number.

Mixed two-way ANOVA without replication (Random variables* are the number of digs needed to complete a nest.)								
Fixed treatment	Random treatment ♀ body wt. in kg							
	4.56	4.20	3.74	4.73	3.06	2.64	3.20	3.09
Nest 1	92	104	90	99	117	94	174	85
Nest 2	216	176	224	185	314	273	242	252
Nest 3	267	231	203	237	328	279	273	207

Results of the ANOVA

Source of variation	D.F.	SS	MS	F	Decision ($\alpha.05$)
Random treatment, ♀ size	7	23.21	3.32	3.05	Fail to reject
Fixed treatment, nest number	2	150.86	75.43	69.20	Reject
Error	14	15.20	1.09		
Total	23	189.27			

F.05 (2) 7, 14 = 3.38

F.05 (2) 2, 14 = 4.86

Newman-Keuls multiple range test

Comparison	Difference	SE	q	P	q 0.05,21
Nest 1 vs nest 3	5.59	.60	9.32	3	3.58
Nest 1 vs nest 2	5.00	.60	8.33	2	2.95
Nest 2 vs nest 3	.59	.60	0.98	2	2.95

Conclusion

Nest 1 < nest 2 nest 3

More digs are required to complete nests 2 and 3 than nest 1.

*The square root transformation was used on each random variable before the actual analysis was performed.

Table 14. Results of tests performed to determine if the frequency of weaving, comfort movements, or aggression within a pair was influenced by the phenotype of the male partner.

Null hypotheses	Random * variable	Type of analysis	No. of pairs examined	Decision
1) The occurrence of weaving movements (including turning motions performed after a digging bout) is not influenced by a) the color pattern or b) the relative size** of the male partner.	No. of weaving motions performed during the last hr that the second nest was under construction.	Mann-Whitney U Tests	a = 16 b = 18	a -- Fail to reject H_0 $U=35 < U_{0.05(2)} 6, 10 = 49$ b -- Fail to reject H_0 $U=50 < U_{0.05(2)} 9, 9 = 64$
2A) Neither the a) color pattern, nor b) the relative size of the male partner influenced the number of comfort movements performed while the second nest was under construction.	Total no. of comfort movements.	Model I Two-way ANOVAs with unequal but proportional sub-class numbers.	a = 7 b = 7	a -- Fail to reject H_0 $F=0.64 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=0.07 < F_{.05(2)} 1, 10 = 6.94$
2B) Neither sex performs more comfort movements regardless of the a) color pattern or b) relative size of the male partner.	Same as 2A	Same as 2A	a = 7 b = 7	a -- Fail to reject H_0 $F=1.21 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=1.16 < F_{.05(2)} 1, 10 = 6.94$
2C) There is no interaction between a) the color pattern of the male and the sex of the fish performing a comfort movement, or b) the relative size of the male and the sex of the fish performing a comfort movement.	Same as 2A	Same as 2A	a = 7 b = 7	a -- Fail to reject H_0 $F=0.06 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=0.08 < F_{.05(2)} 1, 10 = 6.94$

Table 14. Results of tests performed to determine if the frequency of weaving, comfort movements, or aggression within a pair was influenced by the phenotype of the male partner - continued.

Null hypotheses	Random * variable	Type of analysis	No. of pairs examined	Decision
3A) Neither the a) color pattern nor b) relative size of the male partner influences the occurrence of aggression within a pair.	Total no. of agonistic activities observed while the second nest was under construction.	Same as 2A	a = 7 b = 7	a -- Fail to reject H_0 $F=1.23 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=0.12 < F_{.05(2)} 1, 10 = 6.94$
3B) Neither sex, regardless of a) the color pattern, or b) relative size of the male is more likely to attack its sexual partner.	Same as 3A	Same as 2A	a = 7 b = 7	a -- Fail to reject H_0 $F=0.004 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=0.004 < F_{.05(2)} 1, 10 = 6.94$
3C) There is no interaction between a) the color pattern of the male and sex on aggression within a pair or b) the relative size of the male and sex on aggression within a pair.	Same as 3A	Same as 2A	a = 7 b = 7	a -- Fail to reject H_0 $F=1.00 < F_{.05(2)} 1, 10 = 6.94$ b -- Fail to reject H_0 $F=3.59 < F_{.05(2)} 1, 10 = 6.94$

* Square root transformation was used on raw count data.

** The males either weighed more or less than the female.

Table 15. The results of Fisher's Exact Probability Tests (with Tocher's Modification) used to determine the influence of male color patterns and body size on the occurrence of false spawnings in chum salmon.

Fisher's Exact Probability Test I: The influence of male color patterns on the occurrence of false spawnings.

	Pairs where false spawnings were observed (class I)	Pairs where no false spawnings were observed (class II)	Total
Group I: ♀♀ with ♂♂ partners having the bar pattern	1	16	17
Group II: ♀♀ with ♂♂ partners having the stripe pattern	7	16	23
Totals	8	32	40

Results: The p of obtaining scores more extreme than those observed = .006.

The p of obtaining scores as extreme as those observed = .054.

Therefore, Tocher's ratio (Seigel, 1956 pp. 96 to 104) =

$$\frac{\alpha^* - p \text{ more extreme cases}}{p \text{ of observed cases}} = .804$$

Decision: Reject H_0 that false spawnings occur at the same rate regardless of the color pattern of the male partner.

Fisher's Exact Probability Test II: The influence of male size on the occurrence of false spawnings.

	Pairs where false spawnings were observed (class I)	Pairs where no false spawnings were observed (class II)	Total
Group I: ♀ > than ♂ partner	5	13	18
Group II; ♀ ≤ to ♂ partner	3	23	26
Totals	8	36	44

Results: The p of obtaining scores more extreme than those observed = .039.

The p of obtaining scores as extreme as those observed = .126.

Therefore, Tocher's ratio = .088.

Decision: Fail to reject H_0 that false spawnings occur at the same rate regardless of the relative size of the male partner.

*
 $\alpha = .05$

The occurrence of weaving motions (including turning movements after a digging bout) was also not affected by the phenotype of the male partner (Table 14). As Fig. 19 illustrates (see also Fig. 18) the propensity to weave or turn after a digging bout is reduced as a nest develops, although some females may continue to perform these activities until spawning occurs. Usually, though, as a nest neared completion the most common feminine activities were either probes, digs, or occasional releases of air.¹¹

Both sexes also performed "comfort movements" at approximately the same rate (about once every 5 min throughout nest construction) regardless of the type of pair (Table 14). Moreover, aggression within a pair was also very low and again the phenotype of the male did not influence the occurrence of these activities. Females occasionally attacked or chased their sexual partners after a spawning had occurred, while males tended to nip at their mates prior to spawning. However, neither sex appeared to be more aggressive than the other (Table 14).

The only feminine display whose frequency was influenced by the physical appearance of the male was prolonged crouching. More false spawnings occurred when females were courted by males having a stripe than when they were courted by males possessing the bar color pattern (Table 15). However, the relative size of the male did not influence the occurrence of false spawnings.

¹¹Females sporadically release gas from their air bladders while they develop a nest in an apparent effort to reduce their buoyancy (Groot, personal communication). While performing covering digs they often break the surface with their beaks agape. This ostensibly allows them to swallow atmospheric air and recapture their original buoyancy.

There are several plausible reasons why male phenotypes apparently have little impact on the total occurrence of feminine reproductive activities. In most chum salmon demes spawner densities will be great enough to ensure that several males (if not more) will encounter each female while she constructs a nest. Intuitively too, the energy allocated for each reproductive task a female performs is probably finely adjusted to maximize the production of young. If a female were to spend inordinate amounts of energy attempting to attract males she may lose valuable guarding time or even spend energy needed to deposit her eggs. Moreover, by performing activities that make her conspicuous, a female may not only attract conspecific males but also predatory birds and mammals. Seemingly such predators may prefer females because of the rich horde of nutrients contained within their eggs.

Nevertheless, it is clear that when females are courted by subdominant or relatively small males they prolong nest construction and often will assume crouching postures several times before finally releasing their gametes. The genetic advantages that these potentially expensive strategies confer on females will be discussed later on.

The Effects of Sexual Selection on Females

Intrasexual Competition for Egg Burial Sites

Competition among females for spawning sites may under some circumstances become quite intense. Obviously, when dense aggregations of spawning fish simultaneously occupy a relatively small area only a few females will be able to establish territories. Under these social

circumstances some females may perish without first depositing their eggs (Schroder 1973). Even under conditions where space is seemingly not limiting, competition among females can potentially occur. Innate preferences for spawning locations having certain hydrological characteristics may create localized aggregations of females and interactions among these fish for "favored" egg deposition sites may occur.

Some of the observations made in the experimental stream were directed toward discovering the strategies females employ in establishing and defending their territories. As we have seen, the outcomes of male x male interactions are often strongly influenced by the relative size of the combatants. Hence, some emphasis was placed on assessing whether the relative size of a female influenced her ability to successfully deposit and guard her eggs.

There are several tactics that females can employ while searching for and acquiring a territory. The most conservative one in terms of energy expenditure is to passively move among existing territory-holders (much like a "pin-ball" through a maze of bumpers) until a suitable unclaimed space is discovered. A potentially more costly approach is to attack and evict a resident female from her territory. Presumably the first tactic should be preferred by female salmon since their means of assessing the availability of unoccupied space (either through visual or tactile cues) is restricted to relatively small areas. Without the ability to determine the abundance of potential nest sites the decision to

acquire a territory through an eviction attempt will often be inappropriate. For plainly it does pay to expend any amount of energy fighting over a "nonlimiting commodity." Moreover, in any confrontation between a territorial and nonterritorial female, the territorial fish has much more to lose (the time and eggs it has already invested in its territory) and therefore should be more aggressive or tenacious than its opponent. Consequently, one would anticipate that eviction attempts would infrequently occur and that most of them would end in failure.

Data presented in Table 16 suggest that the above speculations may be correct, as territorial evictions in the experimental stream were rare events, even under high ($\leq 1.66 \text{ m}^2/\text{♀}$) spawner densities. The few fish that were evicted (either by adjacent territorial females or by a previously nonterritorial fish) were often very weak, since the majority died with 60 hr ($\bar{x} = 62.8 \text{ hr}$, $s = 26.5$, $n = 12$) after losing their territories. Furthermore, a Mann-Whitney U test performed on data collected from one section of the experimental stream indicated that "evicted females" neither weighed more nor less than those that had been able to maintain their territories ($U = 203$, $n_1 = 9$, $n_2 = 67$, $p = .12$).

Another, although less direct assessment of the effects of female body weight on the ability to construct nests and deposit eggs yielded similar results. In this case a Model II regression formula [$\hat{y} = -9584.1602 + (3540.0453)(x)$; $n = 41$] was employed to estimate the fecundity of all the females placed into three sections of the experimental stream. These estimates plus the number of eggs every female retained

Table 16. The occurrence of territorial evictions under various densities of spawning chum salmon in the experimental stream.

Instantaneous spawner density (m ² /female)	Total no. of ♀♀ that successfully avoided eviction	Total no. of ♀♀ that were evicted by adjacent, established ♀♀	Total no. of ♀♀ that were evicted by a previously nonterritorial female	Total no. of ♀♀ unable to establish a territory
0.56	68	6	3	7
1.68	21	1	0	6
1.68	25	1	1	1
2.61	18	0	0	0
2.61	18	0	0	0
6.71	7	0	0	0
6.71	7	0	0	0

at death were used to determine the percentage of eggs each fish failed to deposit. Correlation analysis between the body weight of the females and the percentage of eggs they retained showed that the relative size of a female did not influence her ability to deposit eggs, even under conditions where competition for space undoubtedly occurred (Table 17). Instead the ability to successfully spawn under crowded conditions ($\leq 1.66 \text{ m}^2/\text{♀}$) appeared to be linked to how rapidly a female established a territory--for late-ripening or socially inhibited females retained considerably more eggs than earlier-nesting ones (see Schroder 1973, Table 4, p. 23).

While the acquisition and defense of a territory is obviously associated with the potential fitness of a female, so too is the size of her territory. For instance, Groot (personal communication) observed that female sockeye salmon reproducing in areas with high instantaneous spawner densities became "locked" into small territorial spaces. These fish were often seen dislodging and presumably destroying their own eggs while creating new nests. I never witnessed this phenomenon in the experimental stream although in several sections having high spawner densities ($\leq$ to $1.66 \text{ m}^2/\text{♀}$) a few females were observed spawning more than once in the same nest (after each spawning the eggs were slightly buried by typical covering digs). This tactic is less desirable than constructing the usual four to six separate nests as pathogenic infestations or predation events in such "super nests" are likely to destroy most of the eggs. The normal behavioral pattern probably reflects a compromise between the need to spatially separate and provide each egg with

Table 17. The relationship between female size (weight) and egg retention in three sections of the experimental stream where competition for space was acute.

Spawner density (m ² /female)	Degrees of freedom	Correlation coefficient r*	r ²	Conclusion
0.56	81	-.0618	.0038	nonsignificant $r < r_{.05, 81} = .216$
1.05	43	-.1229	.0151	nonsignificant $r < r_{.05, 43} = .294$
1.10	40	-.0696	.0048	nonsignificant $r < r_{.05, 40} = .304$

*Y₁ = body weight in kg.

Y₂ = percentage of the total egg complement retained at death. (The arcsine transformation was used on these percentages before the analyses were performed.)

relatively clean gravel and the energetic costs of creating such an incubation environment and protecting it from other females.

Thus, to optimize progeny survival, each female requires a certain amount of space. Moreover, given the opportunity, a female should attempt to protect as much space around her redd as possible, since this would reduce the likelihood of her eggs being destroyed by neighboring females. Given these needs, one might expect that "large" females would be more successful than comparatively smaller ones in obtaining and protecting such territories because their size would allow them to dominate smaller opponents. However, the results of a Model III two-way ANOVA summarized in Table 18 show that territory size is not influenced by female weight but is strongly affected by spawner density. The less space allocated/female, the smaller the average territory became. This relationship is delineated in the raw data portion of Table 18 which depicts the average territory size in m^2 under different levels of competition.

Prolonged and intense one-on-one confrontations between females rarely occur. At low spawner densities the interactions that do transpire tend to uniformly distribute the females throughout a spawning reach (Schroder 1977). When competition for space becomes more acute territorial borders often overlap or are adjacent to one another. Therefore, when a fish attempts to establish or enlarge a territory under these circumstances she often has to simultaneously interact with two or more rival territory holders. Consequently, under those very conditions where body weight per se could affect overall territory size its

Table 18. Summary of raw data and results of analyses designed to ascertain the influence of female weight and spawner density on territory size in spawning chum salmon.

Summary of data used in a Model III two-way ANOVA (with unequal sample sizes)				
Fixed treatment Spawner density m ² /q	Random treatment			
	Female weight in kg			
	≤3.5	3.6-4.0	4.1-4.5	≤4.6
6.64	30.50*(9.15) n = 4	26.06 (7.82) n = 4	25.63 (7.69) n = 4	32.0 (9.60) n = 2
2.49	16.85 (5.06) n = 10	18.95 (5.69) n = 11	18.09 (5.43) n = 11	20.10 (6.03) n = 24
1.72	7.25 (2.18) n = 2	12.00 (3.60) n = 4	20.60 (6.18) n = 5	16.13 (4.84) n = 16

Results of the ANOVA

Source of variation	D.F.	SS	MS	F	Decision ($\alpha=.05$)
Main effects					
Density	2	1534.961	767.481	12.18	Reject
Female weight	3	122.566	40.855	1.04	Fail to reject
A x B interaction	6	378.231	63.038	1.61	Fail to reject
Explained	11	1931.741	175.613		
Residual	84	3290.758	39.176		
Total	95	5222.499	54.974		

Newman-Keuls multiple range test**

Comparison	Difference	SE	q	p	q.05 84p
6.64 vs 1.72	12.36	1.4576	8.479	3	3.356
6.64 vs 2.49	9.15	1.3224	6.919	2	2.800
2.49 vs 1.72	3.21	1.0369	3.095	2	2.800

Conclusions ($\alpha.05$)

6.64 < 2.49 < 1.72

The average territory size became smaller as the space allocated/q decreased.

*Territories were measured in square feet, the metric equivalent in square meters is enclosed in the adjacent parentheses.

**Compares mean territory size at different spawner densities.

prominence is reduced because it is unlikely that one female (no matter how large) can successfully intimidate and usurp space from two or more "highly motivated" rivals.

Male Expression of Mate Choice

The above observations clearly indicate that females of all sizes have an equal chance of establishing and maintaining territories under a variety of spawner densities. However, some females, either because of their physical condition, color pattern,¹² relative size, behavioral activities, or other attributes may attract more males than others. The advantage attached to being "attractive" is that it increases the number of potential mates a female can choose among. This, in turn, enhances her ability to pick the most socially dominant or largest individual within her vicinity.

Plainly the most attractive females will be those that offer the greatest potential gains in fitness to their male partners. Thus, the decision to ignore or actively court a female could seemingly be based on her fertility, fecundity, willingness to deposit eggs, and the potential characteristics of her young. However, before any of these attributes can play a role in feminine "attractiveness," they must be potentially detectable by males.

¹²Groot (personal communication) reports that the typical white belly color of a female darkens to a smokey-gray or jet-black when she is close to spawning. If this is the case, then males might be more attracted to females with dark ventral surfaces than to those with white ones. As far as I know, no one has yet examined the influence this color shift may have on female attractiveness.

Within the genus Salmo the fertility of a female declines if she is unable to shed her eggs after they have matured (cf., pp. 52 , Chapter II). If the same trend exists in Pacific salmon (Oncorhynchus) then males may be able to predict the fertility of their potential mates, since the physical appearance of a female starts to deteriorate once she reaches maturity. I never arranged situations where males could choose among females based on their state of deterioration. However, the results of the experiments designed to detect temporal changes in female fertility clearly indicated that females remained fertile for extended periods of time (Fig. 21). When a definite decline in fertility did occur, the fish were usually so weak (i.e., they were customarily pinned against picket barriers or barely able to maintain their positions in the experimental stream) that is doubtful whether they could construct nests or spawn. Moreover, preliminary results from an ongoing study suggest that the occurrence of monstrosities or abnormal sex ratios in chum salmon fry are not associated with the length of time a mature female remains in freshwater before she spawns (M. McDowell, personal communication).

Obviously, the retention of gamete fertility and viability in a semelparous organism is of immense value, particularly in a species where competition for limiting resources may delay an animal from reproducing. Therefore, it is not surprising that natural selection has favored females that could successfully reproduce throughout almost their entire adult freshwater lifetimes. Since the connection between female

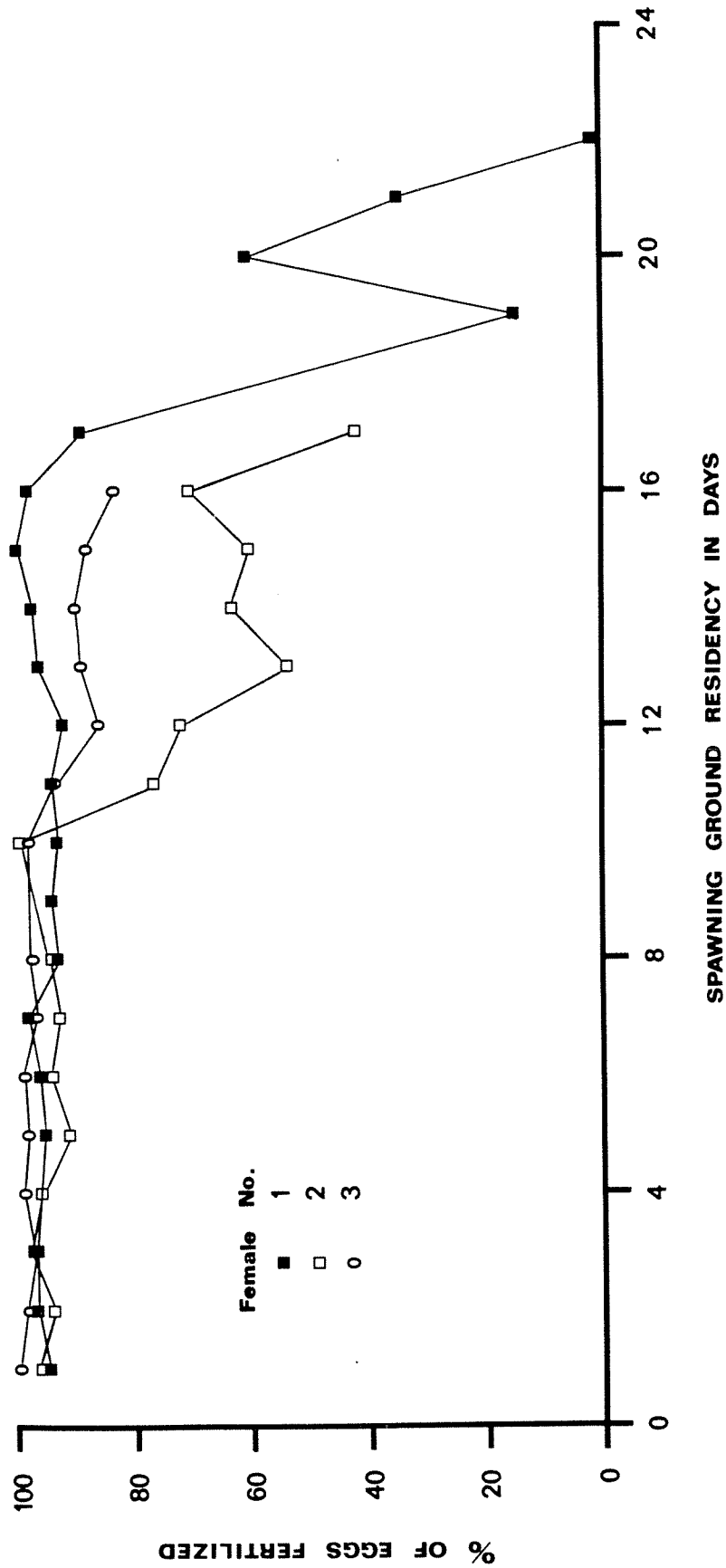


Fig. 21. The effect of freshwater residency on the fertility of three chum salmon females.

appearance and fertility is nebulous (if extant at all), I believe that size plays little if any, part in determining female attractiveness.

As I mentioned earlier (cf., p. 47, Chapter II), the absolute size of a female would seem to be a characteristic that could influence her attractiveness. Indeed, previous observations made by McCart (1970) and Hanson and Smith (1967) suggest that male sockeye salmon may prefer large females as mates. It has long been known that the largest females within a stock have the greatest number of eggs (cf., p. 53, Chapter II). If females place equal numbers of eggs into each of their nests, then those males that spawn with large females will presumably fertilize more eggs than those that have chosen smaller consorts. Moreover, "large" females are usually older than "smaller ones and thus may have larger eggs. Large eggs produce large fry and for reasons previously discussed such fry may enjoy certain antipredation advantages over smaller conspecifics. Finally, older or rapidly growing females (both should be relatively large) may also confer other benefits to their young, e.g., rapid growth, high preemergent survival, and so on (cf., pp. 54-56, Chapter II).

However, when I allowed single males to choose between a "large" or "small" female it became clear that the attractiveness of a female was not strongly influenced by her size. Instead, as Table 19 shows, the males were able to detect often subtle differences in the reproductive status of the two females, and usually paired with the one that was closest to spawning. Although in 4 instances out of 17 females were apparently chosen because of their large size.

Table 19. The results of tests used to determine whether male chum salmon prefer to spawn with "large" or "small" females.

Trial no.	Weight (kg) of the large ♀	Weight (kg) of the small ♀	Time obs in min	Preference and apparent basis of choice
1	5.5	2.6	53	Inconclusive, male courted both females.
2	5.5	2.6	47	Large ♀, based apparently on size.
3	4.3	3.6	120	Small ♀, based on reproductive status.
4	5.5	2.7	45	Large ♀, based apparently on size.
5	4.3	3.6	48	Inconclusive, neither ♀ close to spawning.
6	5.3	3.2	35	Small ♀, based on reproductive status.
7	3.8	3.2	26	Large ♀, based apparently on size.
8	5.9	3.8	35	Large ♀, based apparently on size.
9	5.9	3.8	45	Large ♀, based on reproductive status.
10	5.9	3.8	30	Small ♀, based on reproductive status.
11	5.7	2.6	35	Large ♀, based on reproductive status.
12	5.9	3.8	5	Large ♀, based on reproductive status.
13	5.9	3.8	60	Small ♀, based on reproductive status.
14	5.7	3.8	60	Small ♀, based on reproductive status.
15	5.9	2.6	60	♀ aggression precluded choice.
16	5.9	2.6	30	Large ♀, based on reproductive status.
17	5.7	3.8	40	Small ♀, based on reproductive status.

Summary

10 ♀♀ were chosen on the basis of their reproductive status.
 4 ♀♀ were chosen apparently because of their large size.
 2 trials were inconclusive, either because the male courted both females or both females were quiescent.
 1 trial was invalidated because of female aggression.

While the above experiment was being conducted I noticed that males regularly followed weaving or circling females but usually ignored those that remained motionless. I also observed that males commonly performed prolonged bouts (15 to 30 min) of air gulping when both females appeared to be on the verge of egg deposition. This behavior pattern ceased when the male could discern which female was closer to spawning or when he started to court both fish. These data tend to support the idea that air gulping (at least in males) is a court movement in this species.

Information gathered on the groups of fish placed in the experimental stream to observe overall mating patterns corroborated the notion that a female's "attractiveness" was based almost entirely on her behavior. For instance, when I compared (via two-way ANOVAs without replication) the "attractiveness" of the same female while she was in three separate reproductive states, I found that a fish attracted more males when she was "active" than when she was "wandering" or "spent" (Table 20). These analyses, which utilized data gathered on all the females placed into two sections of the experimental stream, also disclosed that the relative size of a female did not affect her overall "attractiveness."

The above analyses make it clear that the willingness to deposit eggs plays a large role in determining how "attractive" a male finds a female. Therefore any comparison that attempts to test whether variously sized females within the same deme are more or less desirable to males must examine the "attractiveness" of these fish while they are in the same reproductive state. To accomplish this I calculated how

Table 20. The raw data and results of two analyses used to determine if the "attractiveness" of the same female changed because of her reproductive state.

Summary of data used in the first Model III two-way ANOVA without replication												
Fixed treatment (behavior)	Random treatment (q wt in kg)											
	4.05	3.49	3.15	3.15	3.12	3.12	3.12	2.98	2.72	2.69	2.32	
Wandering	4.99	3.04	8.30	4.94	5.66	3.56	6.79	4.53	8.21	4.92		
Active	17.21	16.78	14.25	19.60	19.47	16.78	19.31	13.73	15.89	16.21		
Spent	4.14	3.83	4.65	4.14	7.18	2.32	7.68	4.65	2.71	6.59		

Results of the first ANOVA					
Source of variation	DF	SS	MS	F	Conclusion ($\alpha.05$)
Columns (female wt)	9	41.442	4.61	1.507	Fail to reject H_0
Rows (female behavior)	2	927.857	463.93	151.809	Reject H_0
Error	18	55.006	3.06		

Newman-Keuls multiple range test*

Comparison	Difference	SE	q	p	q.05,18
Active vs spent	12.134	.553	21.942	3	3.609
Active vs wandering	11.429	.553	20.667	2	2.971
Wandering vs spent	0.704	.553	1.274	2	2.971

Conclusions ($\alpha.05$)

Active > Wandering Spent

Active females attract more males than those that are wandering or spent.

Table 20. The raw data and results of two analyses used to determine if the "attractiveness" of the same female changed because of her reproductive state - continued.

Summary of data used in the second Model III two-way ANOVA without replication									
Fixed treatment (behavior)	Random treatment (g wt in kg)								
	4.85	4.62	4.56	4.00	3.86	3.66	3.23		
Wandering	3.61	8.34	2.32	2.85	3.23	3.15	5.98		
Active	13.21	12.72	17.96	14.57	14.12	8.45	12.51		
Spent	6.71	2.75	1.13	1.58	2.46	2.52	2.72		

Results of the second ANOVA						
Source of variation	DF	SS	MS	F	Conclusion ($\alpha.05$)	
Columns (female wt)	6	21.637	3.61	.579	Fail to reject H_0	
Rows (female behavior)	2	458.449	229.23	36.817	Reject H_0	
Error	12	74.715	6.23			

Newman-Keuls multiple range test*					
Comparison	Difference	SE	q	p	q.05, 12
Active vs spent	10.527	.943	11.163	3	3.773
Active vs wandering	9.153	.943	9.706	2	3.082
Wandering vs spent	1.374	.943	1.457	2	3.082

Conclusions ($\alpha.05$)

Active > Wandering Spent

Active females attract more males than those that are wandering or spent.

*Compares the "attractiveness" of females while they are in different reproductive states.

attractive each female within several sections of the experimental stream was, while she constructed nests and spawned. The females within each section were ranked according to their weights; the heaviest third were considered to be "large," while the remaining fish were classified as "medium" or "small" depending on their relative size. One-way ANOVAs (cf., p. 49, Chapter II) were performed on these data to ascertain whether the relative size of a female had any effect on her "attractiveness" while she was sexually active. Once again these tests disclosed that female size per se had little or no effect on her desirability as a potential mate (Table 21).

There are several reasons why every sexually active female should be equally attractive to males. First, as I mentioned earlier, the presence of large aggregations of males around any one female should rarely occur, since it does not pay a male to stay in the vicinity of a female if he has little or no chance of fertilizing any of her eggs. Second, and perhaps just as importantly, the physical appearance of a female, as opposed to her behavioral phenotype, supplies a surprisingly small amount of information to a male.

The following fecundity and egg "size" observations made on female chum salmon returning to Big Beef Creek illustrate this point rather well. As Table 22 shows, there is the expected positive correlation between female weight and absolute fecundity in the chum salmon runs native to this stream. Although these relationships are statistically significant, only 45 to 63% of the variation associated with fecundity

Table 21. Results of statistical analyses designed to determine if the size of a female chum salmon influenced her "attractiveness" while she was sexually active.

Population	$\bar{x}$ OSR	No. of females	Results of one-way ANOVAs (α .05)	Decision
C-5 1975	0.98	16	F = .303 < F 0.05(2) 2, 13 = 4.97	Fail to reject H_0^*
C-11 1975	1.05	14	F = .658 < F 0.05(2) 2, 11 = 5.26	Fail to reject H_0
C-7 1975	1.22	27	F = 2.35 < F 0.05(2) 2, 24 = 4.32	Fail to reject H_0
C-3 1976	1.84	15	F = 1.89 < F 0.05(2) 2, 12 = 5.10	Fail to reject H_0
C-4 1976	3.98	16	F = 2.07 < F 0.05(2) 2, 13 = 4.97	Fail to reject H_0

* Null hypothesis: Sexually active "small," "medium," and "large" females are equally "attractive" to chum salmon males.

Table 22. Results of the correlation analyses used to examine the association between female size (weight log 10) and fecundity in chum salmon returning to Big Beef Creek.

Year	Run	Age at maturity	N	r	r ²	Significant ($\alpha.05$)
1974	Late	3	28	.618	.382	Yes $r > r$, 26 = .374
	Late	4	112	.633	.401	Yes $r > r$, 110 = .186
	Late	3 and 4	140	.719	.517	Yes $r > r$, 138 = .166
1975	Early	3	6	.498	.248	No $r < r$, 4 = .811
	Early	4	1	not enough data		
	Early	3 and 4	7	.671	.451	No $r < r$, 5 = .755
1975	Late	3	6	.649	.421	No $r < r$, 4 = .811
	Late	4	16	.596	.355	Yes $r > r$, 14 = .497
	Late	3 and 4	22	.694	.482	Yes $r > r$, 20 = .423
1976	Early	3	17	.760	.578	Yes $r > r$, 15 = .482
	Early	4	38	.568	.323	Yes $r > r$, 36 = .320
	Early	3 and 4	55	.791	.625	Yes $r > r$, 53 = .266

can be explained by weight alone. Moreover, the absolute fecundity of a female is of little pragmatic interest to males. What really influences their potential fitness is the number of eggs a female deposits during a spawning act.

Recently, Hawke (1978) found that chinook salmon females laid progressively fewer eggs in each of their nests. For example, the first nest often received one fourth ($\bar{x} = 26\%$, S.D. 1%, $n = 7$) of a female's egg complement while her fifth or sixth nest received less than 10% ($\bar{x} = 8\%$, S.D. = 1%, $n = 7$). Female chum salmon appear to deposit their eggs in a similar manner. While examining the gametic contributions of satellite and alpha males, I retrieved all the eggs deposited in the first nests of six females. In every instance, each individual released between 31 and 37% ($\bar{x} = 35\%$, S.D. = .01%, $n = 6$) of her eggs during her first spawning. Since these fish would ordinarily spawn another 3 to 5 times it seems likely that their last nest would contain 1/4 to 1/2 as many eggs as their first nest.

A possible explanation for this phenomenon is that during a spawning act (which consistently lasts for ≈ 10 sec) the female apparently contracts her lateral body walls and simultaneously relaxes the muscles that surround the vent. When the coelomic cavity is full of eggs the internal pressures generated by these muscle movements allow a rapid expulsion of eggs to occur. As a female progresses from one spawning event to the next there should be a decline in these internal pressures and thus fewer eggs will be expelled per unit of time.

No matter how such an egg-laying pattern may occur, its existence makes it difficult for males to estimate the number of eggs a female may deposit during any given spawning act. For instance, a relatively "small" female may lay considerably more eggs into her first nest than a "large" one in her last nest. One might predict then, that males would prefer "active" females that have never spawned over those that are digging their last nests.

Conceivably the body contour and the presence or absence of disturbed gravel areas next to a female could be used as visual cues by males to distinguish "virgin" females from those that have almost finished spawning. However, a human observer has a difficult time associating the body contour of a female with the number of times she may have spawned. Moreover, in a typical spawning reach, the swimming and digging activities of the fish aggregated there tend to universally clean the gravel surface. Hence, in most cases it is probably impossible for a male to determine whether the female he is courting has ever spawned before. Therefore it is unlikely that either the absolute fecundity or the number of times a female has spawned influences her "attractiveness."

The observations made by McCart (1970) on the attractiveness of sockeye and kokanee females (cf., pp. 47-48 , Chapter II) provide an exception to the above generalizations. Female sockeye salmon apparently have ten to twelve times as many eggs as kokanee (McCart 1970). Therefore, a typical kokanee would probably place between 60 to 100 eggs in her first nest while most sockeye would presumably deposit three times

as many eggs in their last nests. Hence natural selection would favor those males that preferred to spawn with sockeye females since by doing so they would fertilize considerably more eggs (see pp. 229-230, for further reasons why sockeye males may prefer anadromous females).

Additionally, McCart (1970) noticed that sockeye females had larger eggs than kokanee ($\bar{x}$ 117 mg vs $\bar{x}$ 79 mg for "eyed" eggs) and this may have contributed to their overall attractiveness. It is doubtful that this trait influences the attractiveness of female chum salmon since the linkage between female size and egg size appears to be weak in this species. For instance, the correlation analyses performed on data collected from chum salmon returning to Big Beef Creek often revealed that less than 20% of the variation associated with egg size could be explained by body size (Table 23). This means that females having very different lengths or weights may produce eggs that are quite similar to one another. Intuitively, this makes sense because the environmental conditions existing within a spawning bed and later on in rearing areas of a population probably favor fry originating from eggs having certain size characteristics. These arguments have been developed before, and I refer the interested reader to Koski (1975) for further details.

The one trait that appears to be connected to the phenotype of a female is her age at maturity. Generally, older females are longer and heavier than those maturing at an earlier age (Table 24). Additionally, the oldest females returning to Big Beef Creek (usually 4-year-olds) tended to have greater absolute fecundities (Table 25) and larger eggs

Table 23. The relationships between female size and egg size in Big Beef Creek chum salmon.

Year	Run	Age at maturity	Traits correlated			N	r	r ²	Significant (α :05)
			Y ₁	Y ₂	*				
1974	Late	3	Wet egg weight	Fish weight		47	.694	.481	Yes r > r, 45 = .288
	"	4	"	"		150	.387	.150	" r > r, 148 = .160
	"	3 and 4	"	"		197	.673	.454	" r > r, 195 = .140
1974	Late	3	Dry egg weight	Fish weight		47	.723	.522	Yes r > r, 45 = .288
	"	4	"	"		150	.432	.187	" r > r, 148 = .160
	"	3 and 4	"	"		197	.691	.477	" r > r, 195 = .140
1974	Late	3	Egg diameter	Fish weight		47	.724	.523	Yes r > r, 45 = .288
	"	4	"	"		150	.335	.112	" r > r, 148 = .160
	"	3 and 4	"	"		197	.660	.435	" r > r, 195 = .140
1974	Late	3	Wet egg weight	Fish length		47	.622	.387	Yes r > r, 45 = .288
	"	4	"	"		150	.308	.095	" r > r, 148 = .160
	"	3 and 4	"	"		197	.642	.413	" r > r, 195 = .140
1974	Late	3	Dry egg weight	Fish length		47	.657	.432	Yes r > r, 45 = .288
	"	4	"	"		150	.367	.134	" r > r, 148 = .160
	"	3 and 4	"	"		197	.663	.439	" r > r, 195 = .140
1974	Late	3	Egg diameter	Fish length		47	.638	.408	Yes r > r, 45 = .288
	"	4	"	"		150	.276	.076	" r > r, 148 = .160
	"	3 and 4	"	"		197	.639	.408	" r > r, 195 = .140
1975	Early	3	Wet egg weight	Fish weight		101	.442	.135	Yes r > r, 99 = .196
	"	4	"	"		6	.286	.032	No r < r, 4 = .811
	"	3 and 4	"	"		107	.477	.228	Yes r > r, 105 = .190
1975	Early	3	Dry egg weight	Fish weight		101	.388	.151	Yes r > r, 99 = .196
	"	4	"	"		6	.105	.011	No r < r, 4 = .811
	"	3 and 4	"	"		107	.446	.199	Yes r > r, 105 = .190
1975	Early	3	Egg diameter	Fish weight		101	.415	.172	Yes r > r, 99 = .196
	"	4	"	"		6	.103	.011	No r < r, 4 = .811
	"	3 and 4	"	"		107	.453	.205	Yes r > r, 105 = .190

Table 23. The relationships between female size and egg size in Big Beef Creek chum salmon - continued.

Year	Run	Age at maturity	Traits correlated				N	r	r ²	Significant ($\alpha.05$)
			Y ₁	Y ₂						
1975	Early	3	Wet egg weight	Fish length			101	.354	.125	Yes r > r, 99 = .196
	"	4	"	"			6	.241	.058	No r < r, 4 = .811
	"	3 and 4	"	"			107	.407	.166	Yes r > r, 105 = .190
1975	Early	3	Dry egg weight	Fish length			101	.336	.113	Yes r > r, 99 = .196
	"	4	"	"			6	.093	.009	No r < r, 4 = .811
	"	3 and 4	"	"			107	.401	.161	Yes r > r, 105 = .190
1975	Early	3	Egg diameter	Fish length			101	.325	.104	Yes r > r, 99 = .196
	"	4	"	"			6	.034	.001	No r < r, 4 = .811
	"	3 and 4	"	"			107	.378	.143	Yes r > r, 105 = .190
1975	Late	3	Wet egg weight	Fish weight			29	.186	.035	No r < r, 27 = .367
	"	4	"	"			65	.270	.073	No r < r, 63 = .244
	"	3 and 4	"	"			94	.484	.234	Yes r > r, 92 = .203
1975	Late	3	Dry egg weight	Fish weight			29	.159	.025	No r < r, 27 = .367
	"	4	"	"			65	.308	.095	Yes r > r, 63 = .244
	"	3 and 4	"	"			94	.492	.243	Yes r > r, 92 = .203
1975	Late	3	Egg diameter	Fish weight			29	.208	.043	No r < r, 27 = .367
	"	4	"	"			65	.254	.065	No r < r, 63 = .244
	"	3 and 4	"	"			94	.491	.241	Yes r > r, 9 = .203
1975	Late	3	Wet egg weight	Fish length			54	.382	.146	Yes r > r, 52 = .268
	"	4	"	"			127	.262	.069	Yes r > r, 125 = .174
	"	5	"	"			6	.194	.038	No r < r, 4 = .811
1975	"	all ages	"	"			187	.584	.341	Yes r > r, 185 = .143
	Late	3	Dry egg weight	Fish length			54	.389	.151	Yes r > r, 52 = .268
	"	4	"	"			127	.318	.101	Yes r > r, 125 = .174
1975	"	5	"	"			6	.253	.064	No r < r, 4 = .811
	"	all ages	"	"			187	.600	.360	Yes r > r, 185 = .143

Table 23. The relationships between female size and egg size in Big Beef Creek chum salmon - continued.

Year	Run	Age at maturity	Traits correlated		N	r	r ²	Significant ($\alpha.05$)
			Y ₁	Y ₂				
1975	Late	3	Egg diameter	Fish length	54	.333	.111	Yes r > r, 52 = .268
	"	4	"	"	127	.256	.066	Yes r > r, 125 = .174
	"	5	"	"	6	.063	.004	No r < r, 4 = .811
	"	all ages	"	"	187	.580	.336	Yes r < r, 185 = .143
1976	Early	3	Wet egg weight	Fish weight	19	.549	.301	Yes r > r, 17 = .456
	"	4	"	"	50	.514	.264	Yes r > r, 48 = .279
	"	3 and 4	"	"	69	.763	.582	Yes r > r, 67 = .237
	Early	4	Dry egg weight	Fish weight	57	.348	.121	Yes r > r, 55 = .261
1976	Early	4	Egg diameter	Fish weight	57	.344	.118	Yes r > r, 55 = .261
	Early	3	Wet egg weight	Fish length	19	.555	.308	Yes r > r, 17 = .456
	"	4	"	"	50	.555	.308	Yes r > r, 48 = .279
	"	3 and 4	"	"	69	.784	.615	Yes r > r, 67 = .237
1976	Early	4	Dry egg weight	Fish length	57	.431	.185	Yes r > r, 55 = .261
1976	Early	4	Egg diameter	Fish length	57	.385	.148	Yes r > r, 55 = .261

*Egg weight 12 hrs after water absorption.

**Egg weight before water absorption.

Table 24. Results of tests used to determine whether there were differences among the lengths and weights of Big Beef Creek female chum salmon maturing at different ages.[†]

Year	Run	Age at maturity	Trait	N	$\bar{x}$	95% CI	Range	Type of analysis	Results
1971	Early	3	Weight*	34	3.160	3.010-3.310	2.523-4.366	"t" test	Reject H_0 : $t_{.05}(2)$, $53 \approx 2.005 < t = 3.87$
		4	"	21	3.683	3.424-3.941	2.183-4.593	"t" test	Reject H_0 : $t_{.05}(2)$, $78 \approx 1.991 < t = 6.64$
	"	3	Length**	45	638.7	630.9-646.5	580-705	"t" test	
1971	Late	4	"	35	677.3	668.7-686.0	600-735	One-way ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $218 \approx 3.76 < F = 41.48$
		5	"	49	3.326	3.141-3.510	2.070-5.075	ANOVA and SNK*** test	
	"	3	Weight	165	4.148	4.064-4.232	2.722-5.585	ANOVA and SNK*** test	
	"	4	"	7	4.330	4.064-4.596	3.941-4.820	ANOVA and SNK*** test	
	"	5	"	53	651.1	640.9-661.4	579-746	ANOVA and SNK*** test	
1974	Late	3	Length	182	701.2	696.9-705.5	627-782	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $239 \approx 3.74 < F = 57.19$
		4	"	7	718.3	706.3-730.3	706-744	ANOVA and SNK*** test	
	Early	3	Weight	81	3.413	3.298-3.527	1.871-5.245	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $436 \approx 3.72 < F = 158.41$
		4	"	341	4.688	4.624-4.752	2.977-6.464	ANOVA and SNK*** test	
	"	5	"	17	4.935	4.567-5.302	3.969-6.889	ANOVA and SNK*** test	
1975	Late	3	Length	103	665.9	660.1-671.7	571-753	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $550 \approx 3.69 < F = 237.86$
		4	"	431	732.7	730.1-735.4	622-804	ANOVA and SNK*** test	
	Early	3	Weight	19	740.2	727.7-752.6	701-783	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $496 \approx 1.965 < t = 8.46$
		4	"	486	3.085	3.051-3.119	2.013-4.763	ANOVA and SNK*** test	
	"	3	Length	12	4.030	3.747-4.314	3.402-4.593	"t" test	Reject H_0 : $t_{.05}(2)$, $551 \approx 1.964 < t = 7.37$
1976	Late	3	Weight	539	638.1	636.0-640.3	559-715	"t" test	Reject H_0 : $t_{.05}(2)$, $113 \approx 1.981 < t = 9.44$
		4	"	14	689.1	674.2-704.1	656-732	"t" test	
	Early	3	Length	46	3.423	3.278-3.567	2.580-4.536	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $341 \approx 3.73 < F = 122.14$
		4	"	69	4.419	4.276-4.562	3.034-5.897	ANOVA and SNK*** test	
	"	5	"	115	660.9	655.8-665.8	605-720	ANOVA and SNK*** test	Reject H_0 : $t_{.05}(2)$, $582 \approx 1.964 < t = 18.27$
1976	Early	3	Weight	221	710.9	706.9-714.9	595-778	"t" test	Reject H_0 : $t_{.05}(2)$, $713 \approx 1.963 < t = 21.29$
		4	"	8	739.6	713.4-765.8	690-799	"t" test	
1976	Early	3	Length	109	3.073	2.995-3.151	2.013-4.479	ANOVA and SNK*** test	Reject H_0 : $F_{.05}(2)$, $582 \approx 1.964 < t = 18.27$
		4	"	475	4.256	4.197-4.314	2.211-6.606	ANOVA and SNK*** test	
1976	Early	3	Weight	130	639.6	635.0-644.2	570-729	"t" test	Reject H_0 : $t_{.05}(2)$, $713 \approx 1.963 < t = 21.29$
		4	"	585	703.6	701.0-706.1	596-810	"t" test	

[†]Some of the fish returning in these runs were used as experimental animals in the mate selection studies.

*Body weights in kilograms.

**Fork lengths in millimeters.

***Student-Newman-Keuls Test, homologous sets are underlined, values increase from left to right.

Table 25. Results of analyses used to assess whether the absolute fecundity of 4-yr-old chum salmon differed from 3-yr-old females returning to Big Beef Creek within the same year and run.

Year	Run	Age at maturity	$\bar{x}$ Fecundity	s	N	Type of analysis	Conclusion
1974	Late	3	3113.2	296.1	35	t-test	Reject H_0 : $t=6.917 > t_{.05(2)155}=1.976$
		4	3620.8	430.2	122		
1975	Early	3	3000.7	321.6	6	none	
		4	3409.0	--	1		
1975	Late	3	2795.0	232.4	8	t-test	Reject H_0 : $t=3.025 > t_{.05(2)26}=2.056$
		4	3252.0	398.2	20		
1976	Early	3	2929.0	339.0	17	t-test	Reject H_0 : $t=5.520 > t_{.05(2)54}=2.005$
		4	3408.0	280.0	39		

(Table 26) than earlier maturing ones. Moreover, maternal age by itself has been linked with certain progeny characteristics (e.g., survival during early development cf., p. 54, Chapter II) in several species of salmonid fishes. Yet for some reason males have not developed a preference for large or old females. This may occur because it is costly in terms of time and energy to search for such mates (see pp. 232-234, Chapter III) or possibly in this species the age of a female is not consistently linked with the performance of her offspring.

Some of the hatchery experiments described in Chapter II were designed to test this last assumption. Furthermore, since females clearly exhibited a preference for large males it was also important to examine the influence of paternal size and age (since as Table 27 shows, these are linked with one another) on progeny characteristics. Consequently, the remaining hatchery experiments were performed to ascertain the advantages a female gains by being selective.

The Results of the Hatchery Experiments Employed
to Determine the Influence of Parental Age
and Size on Progeny Performance

As the above suggests, the principal goal of the hatchery work was to attempt to determine why, from an evolutionary perspective, males were nonselective and females selective about choosing mates with certain phenotypic traits. The hatchery studies were designed to answer this question by ascertaining whether certain observable adult characteristics consistently affected gamete viability and progeny performance. Plainly, in these experiments (Table 28) the incubation and rearing

Table 26. The results of tests used to examine the influence of age-at-maturity on egg size in chum salmon returning to Big Beef Creek.

Year	Run	Age at maturity	Trait*	n	$\bar{x}$	95% confidence intervals	Results of t-tests
1974	Late	3	Dry egg wt	47	87.98	85.50- 90.47	Reject H_0
"	"	4	" " "	150	104.70	103.07-106.33	$t=10.267 > t_{.05(2)195}=1.973$
"	"	3	Egg diam	47	6.72	6.66- 6.79	Reject H_0
"	"	4	" "	150	7.16	7.12- 7.20	$t=10.993 > t_{.05(2)195}=1.973$
1975	Early	3	Dry egg wt	101	90.39	88.74- 92.05	Reject H_0
"	"	4	" " "	6	103.15	93.16-113.14	$t=3.602 > t_{.05(2)105}=1.983$
"	"	3	Egg diam	101	6.84	6.83- 6.85	Reject H_0
"	"	4	" "	6	7.12	7.04- 7.21	$t=3.108 > t_{.05(2)105}=1.983$
1975	Late	3	Dry egg wt	54	88.31	85.95- 90.67	Reject H_0
"	"	4	" " "	127	105.00	103.21-106.79	$t=10.505 > t_{.05(2)179}=1.973$
"	"	3	Egg diam	54	6.80	6.74- 6.87	Reject H_0
"	"	4	" "	127	7.23	7.19- 7.28	$t=11.237 > t_{.05(2)179}=1.973$
1976	Early	3	Wet egg wt**	52	222.8	213.31-232.29	Reject H_0
"	"	4	" " "	53	268.6	262.41-274.79	$t=48.603 > t_{.05(2)71}=1.994$

*All weights in mg.

All diameters in mm.

**Wet weight of egg before water absorption.

Table 27. Results of analyses used to ascertain whether there were differences among the lengths and weights of male chum salmon returning to Big Beef Creek in the same year but maturing at different ages.[†]

Year	Run	Age at maturity	Trait	N	$\bar{x}$	95% CI	Range	Type of analysis	Results
1971	Early	3	Weight*	24	3.799	3.524-4.075	2.835-4.989	t-test	Reject H_0 : $t.05(2)43=2.017 < t=3.01$
"	"	4	"	21	4.377	4.089-4.664	3.317-5.500		
"	Early	3	Length**	30	683.4	669.2-697.6	626-751	t-test	Reject H_0 : $t.05(2)62=1.999 < t=5.44$
"	"	4	"	34	729.1	718.9-739.2	674-791		
1971	Late	3	Weight	42	3.595	3.347-3.843	1.843-5.273	1-way ANOVA & SNK*** test	Reject H_0 : $F.05(2)2,180=3.77 < F=33.26$
"	"	4	"	136	4.890	4.730-5.050	2.694-7.145		
"	"	5	"	5	4.740	4.484-4.997	4.480-5.018		SNK: $\underline{3} < \underline{5} < \underline{4}$
"	Late	3	Length	48	672.7	660.4-685.0	547-747	1-way ANOVA & SNK test	Reject H_0 : $F.05(2)2,201=3.76 < F=53.21$
"	"	4	"	151	743.1	736.5-749.8	635-835		SNK: $\underline{3} < \underline{5} < \underline{4}$
"	"	5	"	5	737.0	721.7-752.3	725-756		
1974	Late	3	Weight	85	3.853	3.694-4.012	2.211-5.358	1-way ANOVA & SNK test	Reject H_0 : $F.05(2)2,420=3.72 < F=147.37$
"	"	4	"	322	5.519	4.683-6.355	2.863-8.193		
"	"	5	"	16	6.102	5.104-7.100	4.310-7.853		SNK: $\underline{3} < \underline{4} < \underline{5}$
1974	Late	3	Length	110	691.4	682.9-699.9	552-768	1-way ANOVA & SNK test	Reject H_0 : $F.05(2)2,578=3.72 < F=264.19$
"	"	4	"	445	778.4	775.2-781.5	634-878		
"	"	5	"	26	794.8	787.5-794.8	735-847		SNK: $\underline{3} < \underline{4} < \underline{5}$
1975	Early	2	Weight	6	2.215	1.862-2.569	1.559-2.693	1-way ANOVA & SNK test	Reject H_0 : $F.05(2)2,422=3.72 < F=40.68$
"	"	3	"	408	3.680	3.623-3.736	2.070-5.273		
"	"	4	"	11	4.997	4.542-5.452	4.508-6.917		SNK: $\underline{2} < \underline{3} < \underline{4}$

Table 27. Results of analyses used to ascertain whether there were differences among the lengths and weights of male chum salmon returning to Big Beef Creek in the same year but maturing at different ages - continued.

Year	Run	Age at maturity	Trait	N	$\bar{x}$	95% CI	Range	Type of analysis	Results
1975	Early	2	Length	8	580.5	558.1-602.9	520-609	1-way ANOVA & SNK test	Reject H_0 : $F_{.05}(2)2,506=3.72 < F=70.80$ SNK: $\underline{2} < \underline{3} < \underline{4}$
"	"	3	"	489	681.2	678.3-684.1	571-763		
"	"	4	"	12	756.3	738.3-774.3	723-833		
1975	Late	3	Weight	60	3.906	3.714-4.097	1.900-5.557	1-way ANOVA & SNK test	Reject H_0 : $F_{.05}(2)2,152=3.78 < F=59.45$ SNK: $\underline{3} < \underline{4} < \underline{5}$
"	"	4	"	90	5.443	5.249-5.636	3.345-7.854		
"	"	5	"	5	6.384	5.636-7.133	5.698-7.173		
1975	Late	3	Length	134	685.0	677.5-692.4	545-780	1-way ANOVA & SNK test	Reject H_0 : $F_{.05}(2)2,353=3.73 < F=161.07$ SNK: $\underline{3} < \underline{4} < \underline{5}$
"	"	4	"	212	759.5	754.4-764.6	621-852		
"	"	5	"	10	810.4	778.5-842.3	767-921		
1976	Early	2	Weight	3	1.852	1.745-1.960	1.814-1.900	1-way ANOVA & SNK test	Reject H_0 : $F_{.05}(2)2,394=3.72 < F=135.17$ SNK: $\underline{2} < \underline{3} < \underline{4}$
"	"	3	"	74	3.987	3.804-4.169	1.559-5.670		
"	"	4	"	320	5.683	5.583-5.782	3.147-8.760		
1976	Early	2	Length	3	543.3	517.5-569.2	535-555	1-way ANOVA & SNK test	Reject H_0 : $F_{.05}(2)2,506=3.72 < F=181.98$ SNK: $\underline{2} < \underline{3} < \underline{4}$
"	"	3	"	81	699.8	690.3-709.3	525-774		
"	"	4	"	425	774.6	771.1-778.2	605-874		

+The fish returning in these runs were used as experimental animals in the mate selection studies.

*Body weights in kg.

**Fork lengths in mm.

***Student-Newman-Keuls Test, homologous sets are underlined, values increase from left to right.

Table 28. A listing of the hatchery studies used to examine the relationships between various parental traits and progeny performance in chum salmon.

Stage in life cycle	Progeny characteristic	Parental traits	Text reference
Egg-to-emergent fry	Egg fertilization	Dam and sire size at maturity (weight and length)	73 - 74
	" "	Dam and sire age at maturity (weight and length)	" "
	" "	Egg size (dry weight)	" "
	Mortality before hatching	Dam and sire size at maturity	" "
	" "	Dam and sire age at maturity	" "
	" "	Dam and sire size at maturity	" "
	" "	Dam and sire age at maturity	" "
	Alevin mortality	Egg size (dry weight)	" "
	" "	Dam and sire size at maturity	" "
	" "	Dam and sire age at maturity	" "
	Occurrence of monstrosities	Egg size (dry weight)	" "
	" "	Dam and sire size at maturity	" "
	" "	Dam and sire age at maturity	" "
Post-emergent fry	" "	Egg size	" "
	Rate of embryo development (as reflected by the velocity of yolk material usage)	Sire age at maturity	74 - 77
	" "	Egg size	" "
	Rate of embryo development (as reflected by fry K_D after a set incubation period)	Sire size at maturity	77 - 78
	" "	Sire age at maturity	" "
	" "	Egg size	" "
	Economy of yolk material Usage	Sire size at maturity	78 - 81
	" "	Sire age at maturity	" "
	" "	Egg size	" "
	Size at emergence	Sire size at maturity	81 - 83
	" "	Dam and sire age at maturity	" "
	" "	Dry egg weight	" "
	Growth rate	Sire size at maturity	89 - 90
Post-emergent fry	" "	Dam and sire age at maturity	" "
	" "	Parental growth (as reflected by size)	" "
	" "	Dry egg weight	" "
	Size at the completion of a 14-wk rearing period	Dry egg weight	" "
	Post-emergent mortality during a 14-wk rearing period	Dam and sire size at maturity	90 - 91
		Dam and sire age at maturity	" "
		Dry egg weight	" "

habitats had to be standardized so that any performance differences among the young could be observed. Both environments were made as uniform as possible but they also tended to maximize growth and survival. Consequently, subtle differences between fish produced by different types of parents could have been masked. Additionally, the progeny characteristics that were evaluated (see Table 28) were arbitrarily chosen and thus important performance differences may yet remain to be discovered. In lieu of these considerations the results presented below are at best preliminary, however, they do provide a foundation for some speculative answers as to why male and female salmon have evolved the mate choice mechanisms they possess.

The Influence of Parental Size and Age on Fertility and Progeny Performance Prior to Emergence

Fertility, i.e., the ability to produce zygotes, could not be associated with parental size or egg size (Table 29) although it did vary when fish of different ages were crossed with one another. However, as Table 30 indicates the percentage of nonviable eggs in the types of crosses examined only ranged from 0.2 to 5.4%, except for one case when it equalled 28.5%. If this latter datum is thrown out, then the mean occurrence of nonviability within the families representing the most fertile cross is only 1% higher (1.4 vs 2.5%) than those representing the least fertile one. It is likely that this one incidence of high nonfertility was associated with improper handling or possibly poor sperm quality rather than by a biological incompatibility caused by parental age. One might expect too, that if such an incompatibility did exist,

Table 29. The influence of parental size and egg size on fertility and embryo and alevin mortality in chum salmon.

Parental age and sex		Correlation		d.f.(v)	r	Conclusion ($\alpha.05$)
3	♀	Dry egg wt vs % of eggs fertilized	"	6	.102	Fail to reject H_0
4	♀	"	"	6	-.308	"
3 & 4	♀	"	"	14	.086	"
3	♀	Body wt vs % of eggs fertilized	"	6	.001	Fail to reject H_0
4	♀	"	"	6	.001	"
3	♂	"	"	10	.104	"
4	♂	"	"	10	-.062	"
3	♀	Body length vs % of eggs fertilized	"	6	.061	Fail to reject H_0
4	♀	"	"	6	-.153	"
3	♂	"	"	10	.104	"
4	♂	"	"	10	-.175	"
3	♀	Dry egg wt vs % of fertilized eggs dying before hatching	"	6	.669	Fail to reject H_0
4	♀	"	"	6	-.051	"
3 & 4	♀	"	"	14	.262	"
3	♀	Body wt vs % of fertilized eggs dying before hatching	"	6	.218	Fail to reject H_0
4	♀	"	"	6	.479	"
3	♂	"	"	10	.171	"
4	♂	"	"	10	.029	"
3	♀	Body length vs % of fertilized eggs dying before hatching	"	6	.075	Fail to reject H_0
4	♀	"	"	6	.295	"
3	♂	"	"	10	.301	"
4	♂	"	"	10	-.061	"
3	♀	Dry egg wt vs % of alevins dying before yolk absorption	"	6	.364	Fail to reject H_0
4	♀	"	"	6	.108	"
3 & 4	♀	"	"	14	.322	"
3	♀	Body wt vs % of alevins dying before yolk absorption	"	6	.254	Fail to reject H_0
4	♀	"	"	6	.096	"
3	♂	"	"	10	.261	"
4	♂	"	"	10	.111	"
3	♀	Body length vs % of alevins dying before yolk absorption	"	6	.165	Fail to reject H_0
4	♀	"	"	6	.298	"
3	♂	"	"	10	.424	"
4	♂	"	"	10	.048	"

*All % were transformed with the arcsin transformation.

Table 30. The raw data and results of tests used to determine whether various types of chum salmon crosses (based upon parental age) experienced differing amounts of nonfertility.

Type of parental cross (♀ age before ♂ age)			
3 x 3	3 x 4	4 x 3	4 x 4
.002*	.004	.010	.008
.012	.004	.013	.010
.013	.007	.021	.010
.014	.008	.025	.012
.015	.011	.026	.017
.017	.014	.041	.023
.021	.015	.054	.027
.026	.020	.285	.031

Results of a Kruskal-Wallis one-way ANOVA used to determine if the occurrence of unfertilized eggs in each of the four types of parental crosses were similar:

$$\text{Reject } H_0 \text{ as } H = 8.6 > \chi^2_{.05, 3} = 7.815$$

Results of the subsequent nonparametric Newman-Keuls multiple range test:

most fertile		least fertile
3 x 4	3 x 3	4 x 4
		4 x 3

* Percentage of unfertilized eggs in each family ($\approx 1,500$ eggs/family).

it would manifest itself throughout the development period. This is clearly not the case, for Tables 29 and 31 show the embryo and alevin mortality in chum salmon are not allied with parental age nor, for that matter, with parental size-at-maturity or egg size. Additionally, Tables 32 and 33 illustrate that the occurrence of monstrosities in the young are also not linked with parental age, size, or egg size.

The effects of various parental traits on how quickly and efficiently their young utilized yolk materials were also examined. Once again, the age of the male parent had no apparent effect on how rapidly his offspring used their yolk materials. However, there was a strong maternal influence, since embryos originating from "large" eggs consumed their yolk materials more rapidly than those originating from small ones (Table 34). The data also suggest that the rate or velocity of yolk consumption per temperature unit remains constant throughout an incubation period.

These results depict a remarkable adaptation that allows embryos fertilized at the same instant but supplied with differing amounts of yolk material to complete their ontogeny at approximately the same time. For example, if on the average ten temperature units are accumulated/day during the spring then the fry originating from the largest and smallest eggs in my experiment would have absorbed all their yolk materials within 8 days of one another (see Table 34). On the other hand, if these embryos had absorbed their yolk materials at the same rate then fry originating from the smallest eggs would have completed yolk absorption almost a month sooner (28 days) than those originating from the largest eggs.

Table 31. Results of Model I two-way ANOVAs used to examine the influence of parental age* on the survival of embryo and alevin chum salmon.

ANOVA no.	Null hypotheses	Source of variation	d.f.	MS	F	Conclusion ($\alpha.05$)
1	The age of the male parent does not affect the % of fertilized eggs dying before hatching.	Sire	1	16.91	1.33	Fail to reject H_0
		Dam	1	2.90	.23	" " "
	The age of the female parent does not affect the % of fertilized eggs dying before hatching.	Interaction	1	6.60	.52	" " "
		Error	28	12.69		
2	The age of the male parent does not affect the % of alevins dying before yolk absorption.	Sire	1	1.39	.44	Fail to reject H_0
		Dam	1	5.92	1.87	" " "
	The age of the female parent does not affect the % of alevins dying before yolk absorption.	Interaction	1	2.72	.86	" " "
		Error	28	3.16		

*3- and 4-year-old fish.

Table 32. The results of a Model I two-way ANOVA used to determine the influence of parental age on the occurrence of monstrosities in chum salmon fry.

Null hypotheses	Source of variation	d.f.	MS	F	Conclusion ($\alpha.05$)
The age of the sire does not affect the occurrence of "monstrosities" in his offspring.	Male age	1	.21	.05	Fail to reject H_0
The age of the dam does not affect the occurrence of "monstrosities" in her offspring.	Female age	1	10.30	2.35	" " "
There is no interaction between sire and dam age on the occurrence of "monstrosities."	Interaction	1	.83	.19	" " "
	Error	28	4.38		

Table 33. The influence of egg weight and parental size on the occurrence of monstrosities in chum salmon fry.

Parental age and sex	Correlation			d.f.	r	Conclusion ($\alpha.05$)	
	Dry egg wt vs percentage* of offspring having a deformity	"	"			Reject H_0	Fail to reject H_0
3 ♀	"	"	"	6	.710	Reject	"
4 ♀	"	"	"	6	-.489	Fail	"
3 & 4 ♀	"	"	"	14	.148	"	"
3 ♀	Body wt vs percentage of offspring having a deformity	"	"	6	.222	Fail	to reject H_0
4 ♀	"	"	"	6	.459	"	"
3 & 4 ♀	"	"	"	14	.207	"	"
3 ♀	Body length vs percentage of offspring having a deformity	"	"	6	.105	"	"
4 ♀	"	"	"	6	.057	"	"
3 ♀	"	"	"	14	.404	"	"
3 ♂	Body wt vs percentage of offspring having a deformity	"	"	10	-.255	Fail	to reject H_0
4 ♂	"	"	"	10	-.188	"	"
3 & 4 ♂	"	"	"	22	-.186	"	"
3 ♂	Body length vs percentage of offspring having a deformity	"	"	10	-.119	"	"
4 ♂	"	"	"	10	-.327	"	"
3 & 4 ♂	"	"	"	22	-.161	"	"

*Percentages transformed with the arcsine transformation.

Table 34. The results of an analysis of covariance designed to examine the influence of egg size and sire age on the rate of yolk material absorption in chum salmon alevins*.

Dry egg wt (mg)	Sire age	N in linear regression formula	Regression coefficient	Slope (mg of yolk used/T.U.)	Estimated no. of T.U.s (C°) required for total yolk absorption
121.35	3	6	.996	-.218	971.24
121.35	4	6	.988	-.209	982.93
100.76	3	6	.997	-.190	931.67
100.76	4	6	.999	-.193	937.62
95.65	3	6	.995	-.178	927.69
95.65	4	6	.996	-.186	916.55
76.93	3	6	.997	-.147	894.49
76.93	4	6	.993	-.146	904.94

Analysis of covariance results

1) Testing for differences among slopes: $F = 14.34 > F_{.05}(2)7,32 \approx 2.74$

Results of the subsequent Newman-Keuls multiple range test for differences in slopes:

greatest consumption/T.U.	smallest consumption/T.U.
-.218 -.209 -.193	-.186 -.178 -.147 -.146

2) Testing for differences in levels: $F = 5.27 > F_{.05}(2)7,39 \approx 2.63$

*All alevins were incubated in 9.4°C artesian water.

No physiological explanation for this phenomenon is available other than the idea that embryos originating from large eggs may have larger cells than those produced by smaller eggs. Conceivably then, these embryos would possess a greater absolute surface area in which to absorb yolk materials.

Even with these differential rates of yolk absorption I found that alevins originating from large eggs generally had more yolk materials and thus higher K_D values than those produced by small eggs at the completion of an incubation period (Table 35). The results of the ANOVAs shown in Table 35 also corroborated the notion that the size and age of a male parent had no influence (as determined by K_D values) on how rapidly his offspring absorbed yolk materials. However, certain parental combinations did produce fry with K_D values that were not necessarily related to egg size alone. Apparently then the rate at which yolk materials are used is influenced by the genotype of the developing fish as well as by the size of the egg it has originated from.

As an alevin utilizes its yolk reserves and develops into a relatively sophisticated organism its ability to convert yolk materials to larval tissue declines (cf., p. 79). Therefore, when I examined the influence that various parental traits might exert on this capability I made sure that the young were in the same stage of development (i.e., had similar K_D values). A randomized block design (Model III two-way ANOVA without replication) was employed to assess the influence that paternal size at maturity might have on how economically chum salmon alevins use their yolk materials. Additionally two similar ANOVAs

Table 35. The results of analyses performed to determine whether egg size, sire age, or size-at-maturity influenced the K_D values of chum salmon fry experiencing identical incubation conditions.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analysis	Type of analysis	Decision
1) The K_D values of fry originating from the same female but sired by "small," "medium," or "large" males are identical.	Cross I	890	Model III two-way ANOVA without replication	Fail to reject H_0 $F=1.92 < F_{.05}(2)2, 16=4.69$
2a) The K_D values of fry originating from the same female but fathered by 2-, 3-, and 4-year-old males are identical.	Cross II	895	Model III two-way ANOVA	Fail to reject H_0 $F=.221 < F_{.05}(2)2, 16=4.69$
2b) The K_D values of fry originating from differently sized eggs are the same when the fry have been incubated under identical conditions.	Cross II	895	Model III two-way ANOVA and a SNK Test	Reject H_0 $F=56.88 > F_{.05}(2)7, 576=2.31$ Results of SNK: * $\frac{1.89}{100} \quad \frac{1.88}{100} \quad \frac{1.86}{87, 91, 92, 83, 79, 78}$
2c) There is no interaction between male age-at-maturity and egg size on the K_D values of chum salmon fry.	Cross II	895	Model III two-way ANOVA	Reject H_0 $F=3.63 > F_{.05}(2)16, 576=1.83$
3a) The K_D values of fry originating from the same female but fathered by 3- and 4-year-old males are identical.	Cross III	886	Same as 2c	Fail to reject H_0 $F=.123 < F_{.05}(2)1, 105=10.00$
		876	Same as 2c	Fail to reject H_0 $F=.056 < F_{.05}(2)1, 8=7.57$

Table 35. The results of analyses performed to determine whether egg size, sire age, or size-at-maturity influenced the K_D values of chum salmon fry experiencing identical incubation conditions - conditions.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analysis	Type of analysis	Decision
3b) The K_D values of fry originating from differently sized eggs are the same when the fry have been incubated under identical conditions.	Cross III	886	Same as 2b	Reject H_0 $F=52.71 > F_{.05(2)5, 288}=2.61$ Results of SNK: 1.91 1.90 1.89 1.88 1.87 1.85 119 93 104 105 117 87
		876	Same as 2b	Reject H_0 $F=8.22 > F_{.05(2)8, 432}=2.22$ Results of SNK: 1.91 1.87 1.87 1.87 1.86 1.86 1.86 1.85 1.83 121 113 96 82 77 85 88 82 93
3c) There is no interaction between male age-at-maturity and egg size on the K_D values of chum salmon fry.	Cross III	886	Same as 2c	Reject H_0 $F=4.78 > F_{.05(2)5, 288}=2.61$
		876	Same as 2c	Reject H_0 $F=45.45 > F_{.05(2)8, 432}=2.22$

*Newman-Keuls multiple range test - used here to compare the K_D values of fry originating from differently sized eggs. The numerator in the depicted results equals the K_D values of the fry while the denominator values represent the dry weight of the eggs (in mg) that the fry originated from.

except with replication and a "paired t" test were used to examine the effect that paternal age might have on this trait.

The results of these analyses (Table 36) plainly show that neither paternal size nor age at maturity per se have any influence on how efficient young chum salmon are in utilizing their yolk materials. However, as Table 36 indicates, the offspring originating from different females vary in their ability to convert yolk materials into body tissues. I could not link this variation to egg size or to female size. In one of the ANOVAs, fry from the smallest eggs proved to be the most efficient while in the other ANOVA fry produced from the largest eggs had this distinction. Maternal weight and length (all the females were 3-year-olds) likewise had no apparent impact on the performance of their progeny. The analyses also showed that certain combinations of parental fish clearly produced alevins that were more efficient than those originating from other crosses. Yet again there were no consistent patterns in the data to enable one to link the efficient use of yolk material to any combination of parental phenotypes.

Essentially the same kind of analyses were used to examine the influence of various parental traits including egg weight on alevin body weight at the completion of an incubation period. As mentioned previously (cf., pp. 81-82, Chapter II), unless size comparisons are made among alevins having similar proportions of yolk and body tissue any inequalities in their weights may merely reflect variation in their developmental stage, rather than true size differences. Consequently, the eggs and subsequent alevins originating from each parental cross were

Table 36. The results of analyses performed to determine whether egg size, sire size, or age-at-maturity influenced how efficiently chum salmon alevins utilized their yolk materials.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analysis	Type of analysis	Decision
1) Alevins produced from the same female but fathered by "small," "medium," or "large" males are equally efficient at converting yolk materials into body tissues.	Cross I	890	Model III two-way ANOVA without replication	Fail to reject H_0 $F=.73 < F_{.05}(2)2, 16=4.69$
2) Alevins originating from the same female but fathered by 3- or 4-year-old males are equally efficient at converting yolk materials into body tissues.	Cross III	886 and 876	Paired "t" Test	Fail to reject H_0 $t = -.92 < t_{.05}(2)14=2.15$
3a) Alevins originating from the same female but fathered by 2-, 3-, or 4-year-old males are equally efficient at converting yolk materials into body tissues.	Cross II	895	Model III two-way ANOVAs* and SNK Tests	1) Fail to reject H_0 $F=1.14 < F_{.05}(2)2, 4=10.6$ 2) Fail to reject H_0 $F=0.16 < F_{.05}(2)2, 4=10.6$
3b) Alevins produced from differently sized eggs are equally efficient at converting yolk materials into body tissues.	Cross II	895	Same as 3a	1) Reject H_0 $F=20.17 > F_{.05}(2)2, 36=4.10$ SNK Results: $\frac{78.4}{86.5} \quad \frac{77.4}{92.1} \quad \frac{75.9}{90.8}$ 2) Reject H_0 $F=17.22 > F_{.05}(2)2, 36=4.10$ SNK Results: $\frac{77.4}{92.1} \quad \frac{77.3}{79.2} \quad \frac{75.1}{82.8}$

Table 36. The results of analyses performed to determine whether egg size, sire size, or age-at-maturity influenced how efficiently chum salmon alevins utilized their yolk materials
- continued.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analyses	Type of analysis	Decision
3c) There is no interaction between male age-at-maturity and egg size on how efficiently alevins convert their yolk materials.	Cross II	895	Same as 3a	1) Reject H_0 $F=8.36 > F_{.05}(2)4$, $36=3.17$ 2) Reject H_0 $F=10.63 > F_{.05}(2)4$, $36=3.17$

* Two separate ANOVAs were performed. The SNK Tests (Newman-Keuls multiple range test) were used to compare how efficiently alevins originating from different females converted their yolk materials into body tissues. The numerator in the depicted results equals the percentage of yolk material converted into body tissue while the denominator represents the dry weight of the eggs (in mg) that the fry originated from.

held for the same length of time in 9.4°C spring water to ensure that the fish would have similar K_D values at the conclusion of an incubation period. However, as was previously seen (Table 35) alevins originating from relatively large eggs generally have higher K_D values than those derived from small ones, even when both types of eggs have accumulated an identical number of temperature units.

The females used to create Crosses I, II, and III had a wide array of egg sizes and thus a randomized block ANOVA (an extension of the "paired t" test) was used to ascertain if alevins produced from the same female (and hence from similar eggs) but sired by various types of males had different dry weights after experiencing identical incubation conditions. The results of these analyses (Table 37) revealed that neither the size nor age of the male parent affected the weight of his offspring.

Even though the eggs used to create the artificial crosses were of various sizes, 14 families in Cross III did produce alevins with similar K_D values (see Table 35). The weight data gathered on these fish were used in an ANOVA (Model III two-way) to ascertain if egg weight affected alevin weight and to detect whether an interaction between sire age and egg weight also influenced alevin size. The results of the ANOVA (Table 37) again showed that male age (the fixed treatment in the analysis) had no impact on the size of his offspring. Moreover, there was no evidence of an interaction between sire age and egg weight on alevin size. However, alevins originating from "large" eggs were clearly heavier than those produced from smaller ones. Correlation analyses were employed to further delineate this relationship and as Table 37 illustrates these

Table 37. The results of analyses performed to determine the influence of egg size and paternal size and age on the weights of chum salmon alevins at the completion of an incubation period.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analysis	Type of analysis	Decision
1) Chum salmon fry produced from the same female but sired by "small," "medium," or "large" males have identical dry weights at the completion of an incubation period.	Cross I	890	Model III two-way ANOVA without replication	Fail to reject H_0 $F = .38 < F_{.05(2)2, 16} = 4.64$
2) Chum salmon fry produced from the same female but sired by 2-, 3-, or 4-year-old males have identical dry weights at the completion of an incubation period.	Cross II	895	Same as 1	Fail to reject H_0 $F = .98 < F_{.05(2)2, 14} = 4.86$
3a) There are no differences in the wet weights of chum salmon fry sired by 3- or 4-year-old males at the completion of an incubation period.	Cross III	876	Model III two-way ANOVA with replication	Fail to reject H_0 $F = .002 < F_{.05(2)1, 6} = 6.20$
3b) There are no differences in the wet weights of chum salmon fry produced from eggs with different dry weights at the end of an incubation period.	Cross III	876	Same as 3a and SNK Test*	Reject H_0 $F = 587.08 > F_{.05(2)6, 336} = 2.45$ SNK Results: Heaviest $\longrightarrow$ Lightest $\begin{array}{r} 3 \\ 4 \\ \hline 113 \end{array}$ $\begin{array}{r} 3 \\ 4 \\ \hline 113 \end{array}$ $\begin{array}{r} 3 \\ 4 \\ \hline 96 \end{array}$ $\begin{array}{r} 3 \\ 4 \\ \hline 96 \end{array}$ $\begin{array}{r} 3 \\ 4 \\ \hline 88 \end{array}$ $\begin{array}{r} 3 \\ 4 \\ \hline 88 \end{array}$

Table 37. The results of analyses performed to determine the influence of egg size and paternal size and age on the weights of chum salmon alevins at the completion of an incubation period - continued.

Null hypotheses	Source of eggs	No. of T.U.s accumulated at time of analysis	Type of analysis	Decision
3c) There is no interaction between sire age and egg size on the wet weights of chum salmon fry just after an incubation period has been completed.	Cross III	876	Same as 3a	Fail to reject H_0 $F=2.36 < F_{.05(2)6}$, $336=2.45$
4) There is no correlation between dry egg weight and wet fry weight at the end of an incubation period.	Cross II	895	Product-moment correlation coefficient	Reject $H_0: r = .974 > r_{.05(2)7} = .666$
	Cross III	876	Spearman's rank correlation coefficient	Reject $H_0: r_s = .967 > r_{s.05(2)7} = .786$

*The SNK Test (Newman-Keuls multiple range test) was used to compare the wet weights of alevins originating from variously sized eggs. The numerator in the depicted results equals the age of the sire while the denominator is the dry weight of the egg (in mg).

tests confirmed the idea that egg weight strongly influences alevin weight.

Besides egg size, the age of the female parent has also been linked to the size of her offspring at emergence. As was mentioned earlier (cf., p. 54, Chapter II) Koski (1975) noticed that eggs with the same diameter but originating from 3- and 4-year-old chum salmon produced fry with different body weights. This observation lead him to speculate that the nutrient content of eggs produced by females with differing life-history strategies may vary from one another. However, several factors which he did not have an opportunity to investigate make this an unlikely event. First, eggs with the same diameter but produced by 3- and 4-year-old fish apparently have differing amounts of yolk material (Table 38), for those produced by 4-year-olds generally have greater dry weights. Therefore Koski's observations may have merely reflected quantitative inequalities in yolk material rather than qualitative ones. Second, the relationship between egg diameter and dry egg weight in chum salmon is surprisingly variable since only 55 to 82% of the variation associated with dry egg weight can be explained by egg diameter (Table 39).

Because the diameter of an egg often disguises the amount of yolk material it contains, I examined the influence of maternal age on progeny size by comparing fry produced from eggs having identical dry weights but taken from females that had matured at different ages. This comparison (a Model I two-way ANOVA) indicated that the size of a chum salmon alevin at the completion of its incubation period was not influenced by

Table 38. The raw data and results of a Wilcoxon Matched-Pairs Signed Ranks Test used to ascertain whether eggs with similar diameters but produced by fish having different life-history strategies had different dry egg weights.

Egg diameter class (mm)	Dry egg weight (mg)					
	Female age			d	Rank of d	Rank with less frequent sign
	3	4	4			
	n	$\bar{x}$	S.D	n	$\bar{x}$	S.D
7.21-7.23	2	107.6	1	11	107.5	8
6.96-6.94	2	95.8	6	9	97.6	6
6.90-6.88	3	93.0	2	7	95.3	7
6.87-6.85	4	91.3	1	3	107.4	13
6.81-6.79	3	91.2	5	2	94.2	1
6.78-6.76	4	87.7	5	2	95.5	16
6.75-6.73	3	85.9	2	4	98.1	12
					-12.2	-6
						T=1

T = 1

N = 7

Reject H_0 , since $\alpha.05(2):T=2$

H_0 : Eggs produced by 3- and 4-year-old females will have similar dry weights if they have identical diameters.

Table 39. The correlation between dry egg weight and egg diameter for chum salmon returning to Big Beef Creek.

Year	Run	♀ age	n	r	r ²	Decision ($\alpha.05$)
1974	Late	3	47	.871	.759	Reject H ₀
1974	Late	4	150	.743	.552	" "
1975	Early	3	101	.891	.793	" "
1975	Early	4	6	.890	.792	" "
1975	Late	3	29	.905	.819	" "
1975	Late	4	65	.881	.775	" "
1976	Early	4	57	.906	.821	" "

the age of its female parent (Table 40). As expected, the analysis also disclosed that the heaviest eggs produced the largest fry. Moreover, the interaction term was significant. However, this result was difficult to interpret because of the small number of egg sizes examined. One possible explanation is that there is variation in the quality of the eggs produced by different females regardless of their age at maturity. Most likely the availability of food and other environmental factors during the time of egg formation play roles in determining gamete quality.

The Influence of Parental Size- and Age-at-Maturity on Offspring Performance after Emergence

The above experiments demonstrated that the size and age of parental fish have no predictable impact on the survival, growth, or size of their offspring from fertilization to yolk absorption. Artificial Crosses I and III were made primarily to determine the importance of various parental phenotypes on the growth and survival of young chum salmon after emergence.

The maternal half-sib families produced by Cross I were used to examine the influence of parental size on juvenile growth during the first 7 wk of exogenous feeding. The data collected on these families (Table 41) showed that in five cases out of eight half-sibs fathered by "large," "medium," and "small" males grew at the same rate. In the remaining three cases, some of the half-sib families did grow at different rates. However, these differences were probably brought about by fortuitous genetic combinations and not by the size of the male parent for in each instance a differently sized male (i.e., a "large," "medium," and

Table 40. The effects of maternal age on the dry weight of chum salmon fry originating from eggs with identical dry weights.

ANOVA Design			
Fixed treatment I: Dry egg weight (mg)	Fixed treatment II: Female age at maturity		
	3	4	
105	3.989 g [*]	3.871 g	
88	3.229 g	3.266 g	

Results of the ANOVA	
Null hypotheses	Decision ($\alpha.05$)
Maternal age has no effect on fry size	Fail to reject H_0 : $F=3.563 < F.05(2)1$, $36=5.47$
Egg size has no effect on fry size	Reject H_0 : $F=1011.94 > F.05(2)1$, $36=5.47$
There is no interaction of maternal age and egg size on the dry weight of chum salmon fry	Reject H_0 : $F=13.048 > F.05(2)1$, $36=5.47$

^{*}Total dry weight of 50 fry.

Table 41. Results of the analysis of covariance tests used to ascertain the influence of male size on the growth rates of maternal half-sib families.

Family no. (dam-sire)	Sire wt (kg)	Slope of the regression line	% daily gain in dry wt	Results of the analysis of covariance and SNK tests ($\alpha.05$)
1-1	2.722	.1154	3.87	No difference in regression slopes.
1-2	4.961	.1026	3.43	
1-3	6.832	.1016	3.40	
2-1	2.722	.1194	4.01	No difference in regression slopes.
2-2	4.961	.1127	3.78	
2-3	6.832	.1126	3.77	
3-4	2.211	.1118	3.75	No difference in regression slopes.
3-5	4.706	.1037	3.47	
3-6	7.541	.1090	3.65	
4-4	2.211	.1076	3.60	No difference in regression slopes.
4-5	4.706	.1040	3.48	
4-6	7.541	.1042	3.49	
5-4	2.211	.1210	4.06	Difference in slopes. <u>small σ^2</u> > <u>medium σ^2</u> > <u>large σ^2</u>
5-5	4.706	.1031	3.45	
5-6	7.541	.0956	3.19	
6-7	3.062	.1214	4.07	Difference in slopes. <u>medium σ^2</u> > <u>small σ^2</u> > <u>large σ^2</u>
6-8	4.848	.1405	4.73	
6-9	8.165	.1077	3.60	
7-7	3.062	.1209	4.06	No difference in slopes.
7-8	4.848	.1269	4.26	
7-9	8.165	.1195	4.01	
8-7	3.062	.1120	3.75	Difference in slopes. <u>large σ^2</u> > <u>small σ^2</u> > <u>medium σ^2</u>
8-8	4.848	.1104	3.70	
8-9	8.165	.1234	4.14	

"small" individual) produced the fastest growing half-sib family (see Table 41).

Data gathered on the families produced by Cross III were used to examine the influence of parental age, size, and egg size on progeny growth and survival. An analysis of covariance performed on some of this information indicated that fish from the various families did grow at different rates ($F = 5.79 > F_{.05(2) 30, 2263} = 1.57$). However, these differences could not be associated with parental age, for none of the maternal half-sib families (two/female - one sired by a 3- and the other by a 4-year-old fish) grew at different rates and only two out of eight sets of paternal half-sib families (two/male - one produced by a 3- and the other by a 4-year-old female) exhibited disparate growth (Table 42). Once again these differences were most likely the consequence of serendipitous combinations of parents as an analysis of covariance that compared pooled regression lines could not reject ($F = .73 < F_{.05(2) 3, 457} = 3.14$) the notion that fry produced from the four possible (i.e., 3 x 3, 3 x 4, 4 x 3, and 4 x 4) parental age combinations had similar growth rates.

Correlation analyses (Table 43) were used to investigate the influence of parental size and also egg size on early growth. These analyses revealed that dam and sire size had no effect on how rapidly their offspring grew. Furthermore, the size of the egg an individual originated from had no apparent impact on how rapidly it grew during the rearing experiment. Finally, the analyses (Table 44) that examined the influ-

Table 42. The importance of parental age-at-maturity on the growth of young chum salmon.

Population	Age of dam	Age of sire	Maternal half-sib families		Fail to reject H_0 that slope 1-1 = 1-2	Results of Newman-Keuls multiple comparison tests ($\alpha.05$)
			Regression slope	% daily gain in dry body wt		
1-1	4	3	.1043	3.49		
1-2		4	.1069	3.58	"	"
2-1	4	3	.1066	3.57	"	"
2-2		4	.1057	3.54	"	"
3-1	4	3	.1001	3.35	"	"
3-2		4	.1082	3.62	"	"
4-1	4	3	.1021	3.42	"	"
4-2		4	.1115	3.73	"	"
5-1	3	3	.1071	3.59	"	"
5-2		4	.1168	3.92	"	"
6-1	3	3	.0985	3.29	"	"
6-2		4	.0970	3.24	"	"
8-1	3	3	.1116	3.74	"	"
8-2		4	.1075	3.60	"	"
9-1	4	3	.1046	3.50	"	"
9-2		4	.1084	3.63	"	"
10-1	4	3	.1073	3.59	"	"
10-2		4	.1009	3.38	"	"
11-1	4	3	.1001	3.35	"	"
11-2		4	.1043	3.49	"	"
12-1	3	3	.0982	3.28	"	"
12-2		4	.1051	3.52	"	"
13-1	3	3	.1048	3.51	"	"
13-2		4	.1096	3.67	"	"
14-1	3	3	.1103	3.69	"	"
14-2		4	.1080	3.62	"	"
15-1	3	3	.1110	3.72	"	"
15-2		4	.1050	3.52	"	"
16-1	3	3	.1050	3.51	"	"
16-2		4	.1071	3.59	"	"

Table 42. The importance of parental age-at-maturity on the growth of young chum salmon - continued.

Population	Age of dam	Age of sire	Paternal half-sib families		Results of Newman-Keuls multiple comparison tests ($\alpha.05$)
			Regression slope	% daily gain in dry body wt	
3-2	4	4	.1082	3.62	Fail to reject H_0 that slope 3-2 = 5-2
5-2	3		.1168	3.92	
10-2	4	4	.1009	3.38	" " " " " 10-2 = 12-2
12-2	3		.1051	3.52	
4-2	4	4	.1115	3.73	Reject H_0 : 4-2 > 6-2
6-2	3		.0970	3.24	
11-2	4	4	.1043	3.49	Fail to reject H_0 that slope 11-2 = 8-2
8-2	3		.1075	3.60	
11-1	4	3	.1001	3.35	Reject H_0 : 8-1 > 11-1
8-1	3		.1116	3.74	
4-1	4	3	.1021	3.42	Fail to reject H_0 that slope 4-1 = 5-1
5-1	3		.1071	3.59	
3-1	4	3	.1001	3.35	" " " " " 3-1 = 6-1
6-1	3		.0985	3.29	
10-1	4	3	.1073	3.59	" " " " " 10-1 = 12-1
12-1	3		.0982	3.28	

Table 43. The influence of parental size and dry egg weight on chum salmon fry growth during a 14-wk rearing period.

Parental age and sex	Correlation	d.f.	r	Conclusion ($\alpha.05$)
3 ♀	Body wt vs offspring growth rate	6	-.045	Fail to reject H_0
	Length* vs offspring growth rate	6	-.092	" " " "
4 ♀	Body wt vs offspring growth rate	6	-.307	" " " "
	Length vs offspring growth rate	6	-.109	" " " "
3 & 4 ♀♀	Body wt vs offspring growth rate	14	-.227	" " " "
	Length vs offspring growth rate	14	-.218	" " " "
3 ♂	Body wt vs offspring growth rate	9	-.039	" " " "
	Length vs offspring growth rate	9	-.360	" " " "
4 ♂	Body wt vs offspring growth rate	10	.335	" " " "
	Length vs offspring growth rate	10	.429	" " " "
3 & 4 ♂♂	Body wt vs offspring growth rate	21	.243	" " " "
	Length vs offspring growth rate	21	.179	" " " "
3 ♂	Growth rate of progeny vs the dry wt of the egg they originated from	6	-.524	" " " "
4 ♂	Growth rate of progeny vs the dry wt of the egg they originated from	6	-.247	" " " "

*Tip of snout to fork in tail.

Table 44. The influence of parental age-at-maturity, size, and dry egg weight on chum salmon fry mortality throughout a 14-wk rearing period.

Null hypotheses		Source of variation	d.f.	MS	F	Conclusion ($\alpha.05$)
Influence of parental age						
The age of the male parent does not affect the mean mortality rate of reared chum salmon fry.		Sire age	1	.01	.02	Fail to reject H_0
The age of the female parent does not affect the mean mortality rate of reared chum salmon fry.		Dam age	1	.39	.74	Fail to reject H_0
There is no interaction between male and female age on the mean mortality rate of reared fry.		Interaction	1	.00	.00	Fail to reject H_0
		Error	24	.53		
Effects of parental size						
Age and sex	Correlation		d.f.	r	Conclusion ($\alpha.05$)	
3 ♀	Maternal body wt vs mean fry mortality during a 14-wk rearing period.		6	.163	Fail to reject H_0	
3 ♀	Maternal length vs mean fry mortality during a 14-wk rearing period.		6	.091	" " "	
4 ♀	Maternal body wt vs mean fry mortality during a 14-wk rearing period.		6	.406	" " "	
4 ♀	Maternal length vs mean fry mortality during a 14-wk rearing period.		6	.083	" " "	
3 & 4 ♀	Maternal body wt vs mean fry mortality during a 14-wk rearing period.		14	.439	" " "	

Table 44. The influence of parental age-at-maturity, size, and dry egg weight on chum salmon fry mortality throughout a 14-wk rearing period - continued.

Age and sex	Correlation	d.f.	r	Conclusion ($\alpha.05$)
Effects of parental size				
3 & 4 ♀	Maternal length vs fry mortality during a 14-wk rearing period.	14	.329	Fail to reject H_0
3 ♂	Paternal body wt vs fry mortality during a 14-wk rearing period.	9	.103	" " "
3 ♂	Paternal length vs fry mortality during a 14-wk rearing period.	9	-.005	" " "
4 ♂	Paternal body wt vs fry mortality during a 14-wk rearing period.	10	-.062	" " "
4 ♂	Paternal length vs fry mortality during a 14-wk rearing period.	10	-.001	" " "
3 & 4 ♂	Paternal body wt vs fry mortality during a 14-wk rearing period.	21	.020	" " "
3 & 4 ♂	Paternal length vs fry mortality during a 14-wk rearing period.	21	.028	" " "
Influence of dry egg weight				
Age	Correlation	d.f.	r	Conclusion ($\alpha.05$)
3	Dry egg wt vs fry mortality during a 14-wk rearing period.	6	-.071	Fail to reject H_0
4	Same as above	5	.022	" " "
3 & 4	Same as above	13	.297	" " "

ence of parental size, age, and egg size on fry mortality during the course of the rearing experiment disclosed that these traits had little or no effect on fry viability.

Some Final Thoughts Regarding Mate Choice in Chum Salmon

The results of the above experiments showed that the physical attributes of males and females provide very little information about the performance of their offspring during incubation or immediately thereafter. These results are not unexpected, for quantitative genetic theory predicts that the amount of additive variance (or "breeding value") associated with traits closely allied with fitness (such as early growth, viability, etc.) should be nonexistent (Falconer 1960; Lannan 1976; Maynard-Smith 1978). Consequently the evolution of female choice in chum salmon, where males provide their offspring with nothing except genetic material, is a definite enigma. This puzzling situation is apparently widespread because unmistakable female preferences for certain types of mates have been observed in many other species where paternal care is nonexistent. Faced with this conundrum, Maynard-Smith (1978, p. 171) makes an important theoretical concession by stating female choice under these circumstances can only be explained by admitting "...the additive heritability of fitness is not zero..."

Evidence presented by Ricker (1972) and more fully synthesized by Frey (personal communication) suggests that life-history strategies in Pacific salmon tend to be sex-linked. That is, males generally produce sons that have life-history strategies similar to their own, while females usually adopt the same maturity schedule as their mothers (see pp. 58-60, Chapter II). Frey (personal communication) hypothesized that the trait under genetic control was the size a maturing fish must reach before it starts its spawning migration, rather than its absolute age. Using this concept one can envision that a population of salmon is represented by an array of genotypes (or size thresholds) that dictate when a fish should leave its ocean feeding grounds and return to its natal stream. Obviously a temporal element must enter into this scenario as fish returning at the wrong time but having the right body size would soon experience genetic bankruptcy. Consequently, there must be migration windows that open only during narrow periods of time. It is during these time-place events that a fish must decide whether to migrate toward its home stream or continue to feed in the open ocean.

The determination of maturity by such a system would seemingly provide several advantages. In particularly good years a fish would probably reach its size threshold one year sooner than expected and thereby avoid the cost of remaining at sea. On the other hand, in poor years an individual would be prevented from returning to freshwater before its body could withstand the rigors of upstream migration or sexual selection on the spawning grounds. No matter what genetic mechanism is employed, this proclivity for sex-linked perpetuation of life-history strategies

potentially provides both sexes with some information about the kinds of sons or daughters their potential mates are likely to produce.

Commonly over 90% of the males returning to Big Beef Creek reproduce as 3- or 4-year olds (see Table 1, pp. 95-97 , Chapter III.) This predominance of two masculine life-history strategies is probably typical of most chum salmon stocks. For convenience, we can label these strategies as "young" (in some northern stocks "young" males may be 4 or more years old) and "old." By preferentially mating with "old" males a female would presumably produce fewer (her sons would experience one more year of marine mortality) but most likely larger sons than one that mated with younger males. The risks associated with producing an older and larger son are relatively small since on the average a chum salmon 30 cm or longer experiences a 2% mortality rate/month while residing in the sea (Ricker 1964). This means that if a female can produce x "young" sons she could expect .79x as many "old" sons.

The field data gathered in the experimental stream clearly suggest that the largest and presumably oldest males in a deme will usually have more opportunities to fertilize eggs than smaller ones, even when fertilizations achieved via the satellite strategy are taken into consideration. This fact plus the apparent similarity between father and son life-history strategies may very well have precipitated a feminine preference for large or socially dominant males.

Clearly there must be costs associated with being large for otherwise it would seemingly pay males to become larger and larger. Cer-

tainly periodic droughts and subsequent reduction in stream flows could create strong selection pressures for smaller body sizes (see McCart 1970). Under low flow conditions large individuals might find migration and reproduction difficult; moreover, their very size would make them conspicuous targets for predators. Falconer (1960) also has suggested that there are often negative correlations between traits that are closely linked to fitness. He mentions that large size in mice, for example, is negatively correlated with alertness. While it is true that large mice are more fecund and better able to produce offspring, their lethargic responses to environmental stimuli make them more susceptible to predation than smaller and more alert mice. Consequently, body size in mice undoubtedly represents a compromise between many sets of negatively correlated traits. The same thing is probably true in chum salmon.

Additionally, the potential fitness of each male is dependent to a large extent on the size and strength of his sexual rivals and not on his absolute weight or length. Hence, female choice should be based primarily upon the social status of her possible mates rather than on their size. Therefore it is not surprising that masculine color patterns appear to influence the reproductive behavior of females more so than male length or weight. If an alpha male for example, possesses the stripe pattern he unwittingly conveys to the female that he is either intimidated by a nearby rival or frightened by the persistent attacks of satellite males. In both instances his potential mate can detect his unease (an impossibility if she relied on male size alone) and delay nest construction. As was mentioned earlier this simple tactic increases the

likelihood of her being discovered by additional and possibly more powerful males or at least forces the alpha male to fend off all the males that encounter the female over a relatively prolonged period of time. Conversely if an alpha male possesses the bar color pattern it is likely that he is the best male in the vicinity and the female should attempt to construct her nest and spawn as quickly as possible. Again, this would be something a female would be unable to determine by simply assessing the size of a male.

There are several theoretical reasons why males are not as selective as females about choosing older or larger mates. First, there is no connection between size and spawning participation in female chum salmon, that is "large" and "small" females ostensibly have an equal chance of depositing their eggs. Consequently, the only advantage a male might achieve by mating exclusively with relatively large and old females is that his subsequent daughters would have greater absolute fecundities (e.g., 4-year-old chum salmon returning to Big Beef Creek have $\approx$ 500 more eggs than 3-year-old females) and larger eggs. However, to be selective a male has to "know" what is available to him. And this requires searching time, an expensive commodity for a semelparous organism reproducing in an environment that precludes long-range evaluation of females.

A hypothetical example will help to put the cost of being selective into proper perspective. Imagine two males, one "selective" and the other "nonselective" reproducing in a deme where 75% of all the sexually

active females are "old", i.e., acceptable to the choosy male. Assume that the nonselective male utilizes 4 hrs/spawning (2 hrs for courting plus an additional 2 hrs for searching) and that he is sexually active for 15 days or involved in 90 spawnings. Since a quarter of the female population is unacceptable to the choosy male his "searching time" should be 25% longer and hence it will take him 4-1/2 hrs to complete a spawning. Suppose further that "old" females have an average fecundity of 3,500 eggs while "young" ones produce 3,000 ova and that each female will spawn six times. On the average then the selective male will fertilize 583.3 eggs/spawning (i.e., $3,500/6$) whereas the nonselective one will inseminate approximately 20 eggs less/mating [i.e., $(.75)(3,500)/6 + (.25)(3,000)/6 = 562.5$]. Thus at the conclusion of his reproductive life our nonselective male will have fertilized 50,625 eggs (90 spawnings x 562.6) while the selective one will have inseminated 46,664 eggs (80 spawnings x 583.3).

In most North American streams 90% of these eggs will perish before they emerge from the streambed (Wickett 1952; Hunter 1959; McNeil 1962; Lister and Walker 1966) and only 1% of the subsequent surviving fish will reach maturity. If half of the mature fish are females and the progeny of "young" and "old" females survive at equal rates because of egg size differences¹³, then the daughters originating from the nonselective male should produce 85,421 eggs (25.31 daughters x their mean expected fecundity or 3,375 eggs).

¹³"Old" females generally produce larger eggs than "younger" ones and therefore I have assumed that the cost associated with remaining at sea for an additional year (i.e., a 2% monthly mortality rate) equals the benefit derived from originating from a large egg.

Recall that the ultimate reason for being selective was to produce daughters with relatively high fecundities. Plainly a selective male will sire fewer daughters because he spends more time searching for suitable mates. Consequently, in order for this strategy to coexist or become predominate within a population, the daughters of a selective male must produce the same or more eggs than those derived from nonselective rivals. Under the assumptions of our hypothetical example this does not occur since the daughters originating from the selective male are expected to produce 81,655 eggs ($23.33 \times 3,500$) or approximately 4% fewer ova than the females fathered by the nonselective fish.

Using the same assumptions I have plotted (Fig. 22) similar percent gains or losses at three different levels of masculine discrimination under varying conditions of female visibility (as measured by the amount of time needed to locate a sexually active female). The resulting data suggest that when females can be rapidly found and evaluated a male could realize a genetic gain by being selective. However, if it takes a nonselective male 1 hr or more to locate an active female then the cost of being selective becomes prohibitive.

The amount of time a male might need to find a female has not been ascertained in this species. Nevertheless, the random distribution of females within a deme, their short sexual life-times and male competition will probably force most males to spend an hour or more in locating each new mate. Tentatively then, there simply does not appear to be a big enough dividend associated with being choosy to pay for the time consumed searching for certain types of females.

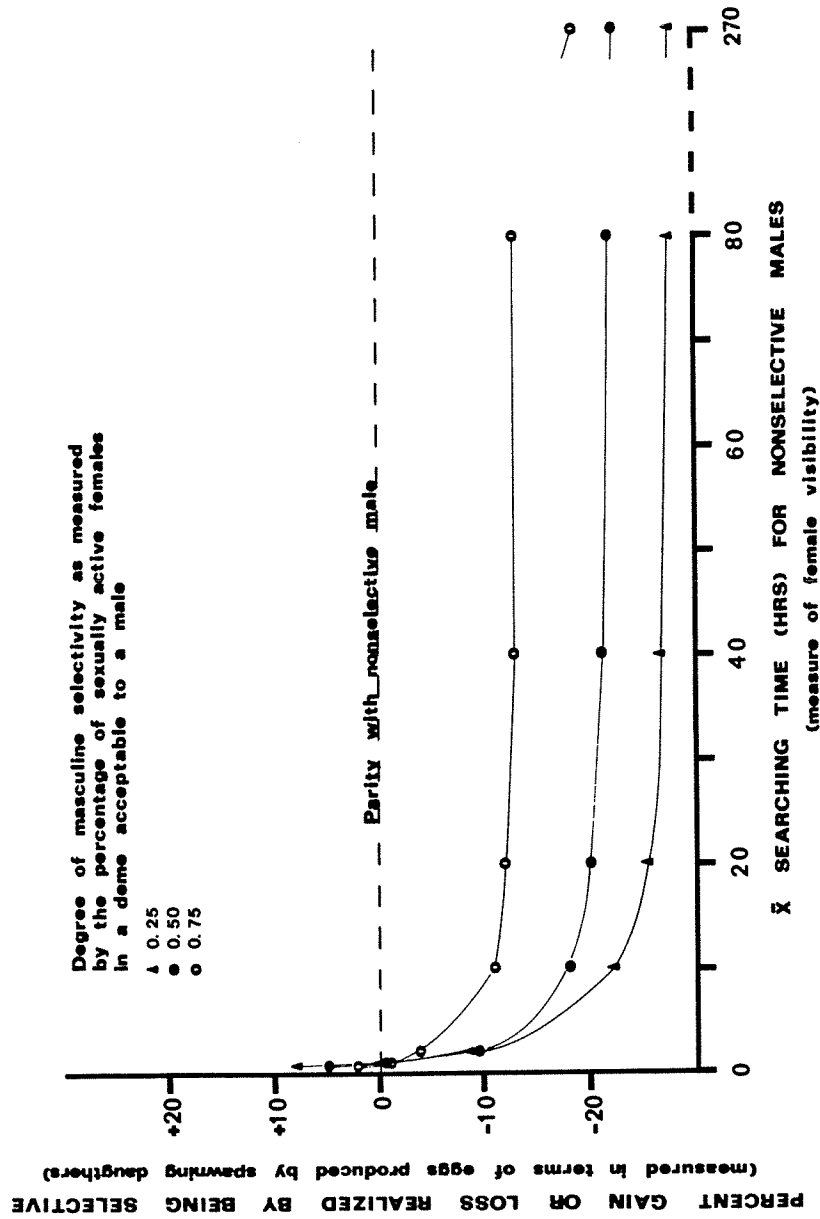


Fig. 22. Hypothetical gains or losses in the potential fitness on "nonselective" and "selective" males under varying degrees of female visibility and acceptability.

Classically, the lack of mate discrimination found in males of many species has been attributed to the small investment this sex makes per mating. This argument could also be applied to salmon. Mathisen (1962) found for instance that sockeye males could successfully fertilize all the eggs deposited by 15 females (≈ 90 spawnings if each female dug six nests). This means that each time a female spawns she invests approximately $1/6$ of her potential fitness into the act while a male may invest less than $1/100$ th of his. Consequently, a male can afford to gamble and mate with a variety of conspecific females, particularly since the additive variance associated with fitness is apparently small.

In conclusion mate choice and subsequently overall mating patterns in this species appear to owe their origins predominately to masculine intrasexual competition and feminine epigamic selection. In their rush to fertilize as many eggs as possible each male has to find and defend as many mates as possible. Meanwhile, females have developed ways to evaluate male competency and preferentially choose the most socially dominant males in their vicinity in an apparent effort to produce equally successful sons. Plainly then chum salmon do not possess innate preferences for mates having phenotypes similar to their own and for reasons previously discussed, I doubt that such a preference exists within any species of Pacific salmon.

CHAPTER IV. SUMMARY

1. Overall mating patterns in chum salmon demes based upon size or age-at-maturity are not strongly influenced by either temporal or spatial factors. All the members of a stock, regardless of their body sizes or age-at-maturity should become sexually active at approximately the same time since it clearly would not pay an individual to reach sexual maturity before or after most of its contemporaries. Consequently, the total temporal isolation of one age group (or brood year) from another rarely happens in nature, although instances of partial isolation have been observed. However, since males remain sexually active for prolonged periods (10 to 18 days) potential gene exchange among fish arriving into a stream at different times can be high. Aggregations of fish with similar body sizes caused by geological features (e.g., waterfalls) within a stream are also unlikely because: 1) chum salmon usually spawn intertidally or within the first several kilometers of their natal streams, 2) females with different body sizes are often ready to spawn soon after reaching freshwater and appear to prefer spawning sites with similar hydrological characteristics, and 3) sexually mature males search for females and this tends to increase the likelihood that fish of different sizes or ages will encounter one another during a spawning season.
2. On the other hand, both components of sexual selection play prominent roles in determining overall mating patterns. The most important of these appears to be intrasexual competition among males for

females. Because females often deposit their eggs within 36 hr after starting their first nest, they quickly drop out of the pool of reproductively active fish within a deme. Males remain sexually active for a much longer period of time and thus the number of sexually active males/gravid and territorial female (OSR) escalates through time. Such skewed sex ratios strongly influence which males have access to females. For instance, when the OSR within a deme is ≤ 1 every male is equally successful at holding females. However, as the OSR increases, only the strongest males within a deme are able to court females.

3. The ability of a male to defend his mates from rivals depends primarily on his relative size and to a lesser extent on his physical condition. For approximately 70% of a male's reproductive lifetime he can successfully dominate opponents that are nine-tenths his size. When a male approaches death, his ability to defeat smaller opponents slowly decreases. Ritualized fights occur among equally matched males, regardless of their relative body sizes, suggesting that males use factors besides absolute mass to assess the relative strength of their opponents.
4. To circumvent the effects of intrasexual competition subdominant males position themselves in back of pairs and attempt to "steal" fertilizations during spawning acts. The occurrence of such "satellite males" was close to zero when the OSR within a deme was ≤ 1.4 but rose asymptotically to 20% at higher OSRs. Consequently, the number of males associated with a pair (1 to 2 satellites) remained

relatively constant at different OSRs. However, the percentage of pairs within a deme accompanied by satellites rose in an almost linear fashion as the OSR within a deme increased. Thus when a male is dominated by two or three sexual rivals he tends to leave a female rather than stay and occupy a subordinate position. This apparently occurs because satellite males are forced to one side and to the rear of a female and are thus likely to miss seeing when she begins to spawn. Intuitively one would expect that males lying on the peripheral edges of spawning groups would fertilize few if any eggs. The results of electrophoretic analyses used to examine the gametic success of satellite males confirmed this speculation, although those satellite males that were able to spawn with a pair fertilized approximately 25% of the eggs that were deposited.

5. Chum salmon males do not possess territories or participate in parental care. In such species, females are expected to choose their mates on the basis of phenotypic attributes that are variable, difficult to disguise, discernible prior to mating, and correlated with their inclusive fitness. The color pattern and body size of male chum salmon appear to be the only traits that meet all of these criteria.
6. A male's color pattern clearly reflects his social status. The "bar" pattern, consisting of vertical bars that run perpendicular to the long axis of the body is generally worn by dominant males. The stripe pattern, a single black-purple band that is parallel to the long axis and bisects the lateral surface of the fish, is

usually present on territorial females and subordinate males. Both males and females are able to rapidly shift (within seconds) from one pattern to the other. Two divergent selection pressures appear to have favored the refinement and maintenance of these patterns. First in a species where males often attack their sexual rivals it pays females to be conspicuously feminine. Additionally, since males are engaged in the simultaneous "business" of "selling themselves" to females and threatening rivals it is not surprising that the bar pattern which tends to amplify the apparent width of an individual is generally a "masculine" color pattern. Second, current theory predicts that "female mimicry" will occur in a species when competition for females or for resources necessary for successful reproduction is rigged against a segment of the male population. Since females are a limiting commodity in chum salmon demes the use of the stripe pattern by subordinate males probably represents a form of female mimicry. Presumably "female mimics" avoid repeated attacks by other males and can therefore position themselves next to females. This in turn provides them with opportunities to fertilize eggs. The cost of such mimicry lies in the reluctance that females should exhibit to such suitors.

7. Additionally, females are expected to prefer the largest males in a deme since these animals are probably older or have faster growth rates, both of which are signs of vigor and perhaps of a superior genotype. Moreover, within the genus Oncorhynchus males generally produce sons that have similar life-history strategies to their

own. Since larger males usually have more opportunities to fertilize eggs than small ones it would presumably increase the potential fitness of a female if she could produce relatively large sons.

8. A female salmon can theoretically select who spawns with her by delaying nest construction or attacking and chasing undesirable suitors--both strategies lengthen the time a male is forced to defend a female from nearby rivals. She can also enhance her "attractiveness" or advertise her presence by performing motor activities such as digging, weaving, nosing, probing, crouching, etc. in an excessive manner. Videotape films were analyzed to determine whether females used any of these tactics while being courted by various type of males. The tapes revealed that females were "aware" of both the color pattern and relative size of the males that courted them. They slowed down nest construction when courted by males that were smaller than themselves or who possessed the stripe color pattern. The only feminine display (including agonistic behavior) that was influenced by the physical appearance of a sexual partner was prolonged crouching. When courted by males having the stripe pattern this behavior occurred more often than when the male had the bar pattern. The relative size of the male did not influence the frequency of prolonged crouching.
9. Males, on the other hand, were acutely aware of female movements, particularly those like nosing, probing, and crouching where the female's body is angled toward the substrate. Female movements

like weaving and nest digging also appeared to attract males but not as strongly as the above behaviors.

10. Intrasexual competition also affected the "spawning success" of females. Rivalry for territory sites became intense when $\leq 1.66 \text{ m}^2$ was allocated per female in the experimental stream. However, the relative size of a female did not influence her ability to establish or maintain a territory. Furthermore, the amount of space a female could successfully defend was not altered by her relative size but was strongly influenced by the number of territorial females within her spawning reach. Generally the greater the competition for space the smaller the area a female could successfully hold.
11. The relative size of a female also did not influence her "attractiveness" to males. However, males definitely preferred females that were close to spawning over those that were nonterritorial, spent, or who were just beginning a nest. Apparently, the impossibility of predicting the number of eggs a female will deposit, the size of those eggs, the quality of the subsequent young, and the costs incurred by being selective (i.e., time lost by searching) have forced males to adopt the simple strategy of attempting to fertilize as many eggs as possible.
12. Neither female nor male fertility appear to be important in determining how attractive they may be to the opposite sex, primarily

because members of both sexes remain fertile for prolonged periods of time.

13. Previously gathered information on salmonid fishes indicated that parental age and growth characteristics affected the quality of their young. Since females exhibited a behavioral preference for socially dominant and "large" males two artificial crosses (Crosses I and II) were made to determine if any progeny characteristics could be linked to paternal size and age-at-maturity. In Cross I the effect of a male's size on the growth rate of his young was examined, while in Cross II the effects of male age and egg size on the efficiency of yolk material utilization were inspected. Differences in growth and yolk material efficiency were detected, but they were not consistently associated with any of the aforementioned parental traits. A third artificial cross (Cross III) was made to examine the importance of parental age and size-at-maturity on the viability and growth of young chum salmon before and immediately after emergence. No differences in viability were observed, although some of the families produced by this cross did grow more rapidly than others. However, neither parental size nor age-at-maturity could be linked to how rapidly young chum salmon grew.
14. The results obtained from these crosses are not surprising. First, the fish produced from each cross were incubated and raised in artificial environments that tended to maximize their survival and growth. Under such circumstances small differences in fry quality may be masked. Moreover, the criteria used to evaluate fry quality

were arbitrarily chosen and thus important performance differences directly linked to parental phenotypes may yet remain to be discovered. Second, current genetic theory predicts that the amount of additive genetic variance (or breeding value) associated with traits closely linked with fitness (such as most of the ones examined) should be zero. However, in this species, and others where paternal care is nonexistent, females have exhibited strong preferences for certain types of male partners. I feel the feminine preference for socially dominant mates (i.e., relatively old and large males) in chum salmon originated and maintains itself because males tend to mature at the same age as their fathers. Consequently, by mating with such individuals a female increases the probability that her sons will have greater access to females than if she were nonselective.

15. Females within this genus apparently also produce daughters with maturity schedules similar to their own. Nevertheless males do not show any preference for relatively large mates. This nonselectivity has manifested itself for several reasons. Unlike males, the relative size of a female does not influence her ability to successfully spawn. Thus the only advantage a male would accrue by exclusively mating with large females would be that his daughters would likewise be large. The potential benefits derived from siring large daughters are that old and large females generally have more and sometimes larger eggs than smaller ones. However, these advantages seem to quickly disappear if a male spends an inordinate

amount of time locating large mates. Additionally, each time a female spawns she invests approximately $1/6$ of her gametes, while a male may invest $1/100$ or less of his. Consequently, the "need" to be selective is potentially much less in males than it is in females.

16. Generally, overall mating patterns and mate choice in this species, and most likely within the genus, reflect the outcomes of intra-sexual competition among males and epigamic selection by females. There is no evidence of any innate preference for similar appearing mates.

LITERATURE CITED

- Abele, L. G., and S. Gilchrist. 1977. Homosexual rape and sexual selection in Acanthocephalan worms. *Science* 173:81-83.
- Alcock, J. 1975. *Animal behavior: an evolutionary approach*. Sinauer Assoc., Inc. Sunderland, MA. 547 pp.
- Allen, G. H. 1958. Notes on the fecundity of the silver salmon (Oncorhynchus kisutch). *Progr. Fish Cult.* 20(4):163-169.
- Averhoff, W. W., and R. H. Richardson. 1974. Pheromonal control of mating patterns in Drosophila melanogaster. *Behavior Genetics* 4(3):207-225.
- Ayala, F. J., M. L. Tracey, L. G. Barr, J. F. McDonald, and S. Perez-Salas. 1974. Genetic variation in natural populations of five Drosophila species and the hypothesis of the selective neutrality of protein polymorphisms. *Genetics* 77:343-384.
- Ayles, B. G., and A. H. Berst. 1973. Parental age and survival of progeny in splake hybrids (Salvelinus fontinalis X S. namaycush). *J. Fish. Res. Board Can.* 30:579-582.
- Baerends, G. P., and J. M. Baerends-van Roon. 1950. *An introduction to the study of the ethology of cichlid fishes*. Behaviour Supplement 1. viii + 242 pp.

- Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout, Salmo trutta L. J. Fish. Biol. 1:349-353.
- Bailey, M. 1976. The trials and tribulations of the analysis of marked Big Qualicum chum salmon. 1976 Northeast Pacific Pink and Chum Salmon Workshop. Alaska Dep. Fish Game. Pages 129-131.
- Bainbridge, R. 1958. The speed of swimming fish as related to size and the frequency and amplitude of the tailbeat. J. Exptl. Biol. 35:109-133.
- Bakkala, R. G. 1970. Synopsis of biological data on the chum salmon, Oncorhynchus keta (Walbaum) 1792. FAO Fish Synopsis No. 41. Circ. 315. 89 pp.
- Bams, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24(5):1117-1153.
- Bams, R. A. 1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can. 27:1429-1452.
- Barlow, G. W. 1967. Social behavior of a South American leaf fish, Polycentrus schomburgkii, with an account of recurring pseudo-female behavior. Amer. Midland Naturalist 78(1):215-234.

- Barlow, G. W., and W. Rogers. 1978. Female midas cichlids' choice of mate in relation to parents' and to own color. *Biol. Behav.* 3:137-145.
- Beall, E. P. 1972. The use of predator-prey tests to assess the quality of chum salmon Oncorhynchus keta fry. M.S. Thesis, Univ. Washington, Seattle. 105 pp.
- Bell, G. M., and W. S. Hoar. 1950. Some effects of ultra violet radiation on sockeye salmon eggs and alevins. *Can. J. Res. Sect. D. Zool. Sci.* 28(1):35-43.
- Berry, R. J., and M. E. Jakobson. 1974. Vagility in an island population of the house mouse. *J. Zool. Proc. Zool. Soc. London* 173(3):341-354.
- Bilton, H. T. 1970. Maternal influences on the age at maturity of Skeena River sockeye (Oncorhynchus nerka). *Fish. Res. Board Can. Tech. Rep.* 167. 20 pp.
- Bilton, H. T., and D. Jenkinson. 1966. Relationship between egg size and fish size in sockeye salmon (Oncorhynchus nerka). *Fish. Res. Board Can. Manu. Rep. Ser. No.* 848.
- Birman, I. B. 1977. Intrapopulation groupings of the Amur autumn chum salmon, Oncorhynchus keta. *J. Ichthyology* 17(5):741-750.

- Borowsky, R., and K. D. Kallman. 1976. Patterns of mating in natural populations of Xiphophorus (Pisces: Poeciliidae). I: X. maculatus from Belize and Mexico. *Evolution* 30:693-706.
- Brannon, E. L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. *Int. Pac. Salmon Fish. Comm. Prog. Rep.* 12. 26 pp.
- Briggs, J. C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. *Cal. Dep. Fish Game Bull.* 94. 62 pp.
- Burck, W. A. 1965. Occurrence of small chinook salmon in stomachs of spent chinook salmon. *Res. Briefs Fish Comm. Oregon* 11(1):51.
- Cederholm, C. J. 1972. Short term physical and biological effects of stream channelization at Big Beef Creek, Kitsap County, Washington. M.S. Thesis, Univ. Washington, Seattle. 80 pp.
- Childs, E. A., and D. K. Law. 1972. Growth characteristics of progeny of salmon with different maximum life spans. *Exp. Geront.* 7:405-407.
- Clarke, W. C., W. Griffioen, and A. Solmie. 1977. A factorial mating study comparing the fertility of pen reared and wild coho salmon (Oncorhynchus kisutch). *Fish. Mar. Serv. Tech. Rep.* 748. 9 pp.

- Cobbs, G. 1977. Multiple insemination and male sexual selection in natural populations of Drosophila pseudoobscura. Amer. Natural. 111(980):641-656.
- Constantz, G. D. 1975. Behavioral ecology of mating in the male Gila topminnow, Poeciliopsis occidentalis Cyprinodontiformes: Poeciliidae. Ecology 56(4):966-973.
- Cooke, F., G. H. Finney, and R. F. Rockwell. 1976. Assortative mating in lesser snow geese (Anser caerulescens). Behav. Genet. 6(2):127-170.
- Cooke, F., P. J. Mirsky, and M. B. Seiger. 1972. Color preferences in the lesser snow goose and their possible role in mate selection. Can. J. Zool. 50(5):529-536.
- Cooney, R. T., D. Urquhart, R. Neve, J. Hilsinger, R. Clasby, and D. Barnard. 1978. Some aspects of the carrying capacity of Prince William Sound, Alaska for hatchery released pink and chum salmon fry. Univ. Alaska, Fairbanks, Sea Grant Rep. 78-4. 98 pp.
- Cox, C. R., and B. J. LeBoeuf. 1977. Female incitation of male competition: a mechanism in sexual selection. Amer. Natural. 111(978):317-335.
- Crow, J. F., and J. Felsenstein. 1968. The effect of assortative mating on the genetic composition of a population. Eugenics Qtrly. 15:85-97.

- Dahl, K. 1918. Studies of trout and trout waters in Norway (Part 1).
Salm. Trout Mag. 17:58-79.
- Disler, N. N. 1953. Ecological and morphological characteristics of the development of the Amur autumn chum salmon--Oncorhynchus keta (Walbaum). Akademiya Nauk SSSR, Ikhtiologicheskaya Komissiya Trudy Soveshehanii, 1:354-362, in Pacific Salmon: Selected Articles from Soviet Periodicals, Transl. IPST Cat. No. 341 (1961) 33-41.
- Dodge, D. P., and H. R. MacCrimmon. 1971. Environmental influences on extended spawning of rainbow trout (salmo gairdneri). Trans. Amer. Fish. Soc. 100(2):312-318.
- Dominey, W. J. 1980. Female mimicry in male bluegill sunfish--a genetic polymorphism? Nature 284(5756):546-548.
- Donaldson, L. R., and K. Bonham. 1970. Effects of chronic exposure of chinook salmon eggs and alevins to gamma radiation. Trans. Amer. Fish. Soc. 99(1):112-119.
- Donaldson, L. R., and D. Menasveta. 1961. Selective breeding of chinook salmon. Trans. Amer. Fish. Soc. 90(2):160-164.
- Duker, G. J. 1977. Nest site selection by chum salmon (Oncorhynchus keta) in a spawning channel. M.S. Thesis, Univ. Washington, Seattle. 113 pp.
- Edwards, D. C. 1967. Reproduction in Olivella biplicata. Veliger 10(4):297-304.

- Ehrman, L. 1966. Mating success and genotype frequency in Drosophila. Anim. Behav. 14(3/4):332-339.
- Ehrman, L. 1970a. The mating advantage of rare males in Drosophila. Proc. Nat. Acad. Sci. U.S.A. 65(2):345-348.
- Ehrman, L. 1970b. Simulation of the mating advantage in mating of rare Drosophila males. Science 167(3919):905-906.
- Ehrman, L., and E. B. Spiess. 1969. Rare-type mating advantage in Drosophila. Amer. Natural. 103:675-680.
- Eisler, R. 1957. Some effects of artificial light on salmon eggs and larvae. Trans. Amer. Fish. Soc. 87:151-162.
- Ellis, C. H., and R. E. Nobel. 1961. Returns of marked fall chinook salmon to the Deschutes River. Deschutes River genetics experiment. Wash. State Fish Dep. Annu. Rep. 1960. 70:72-75.
- Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley Publishing Co., Reading MA. 493 pp.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 173:215-223.
- Falconer, D. S. 1960. Introduction to quantitative genetics. Oliver and Boyd, Edinburgh and London. 365 pp.

- Farr, J. A. 1977. Male rarity or novelty, female choice behavior, and sexual selection in the guppy Poecilia reticulata Peters (Pisces: Poeciliidae) *Evolution* 31(1):162-168.
- Fisher, R. A. 1958. The genetical theory of natural selection. Dover Reprint, New York. 291 pp.
- Fowler, L. G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. *Prog. Fish Cult.* 34(2):66-69.
- Gall, G. A. E. 1974. Influence of size of eggs and age of female on hatchability and growth in rainbow trout. *Cal. Fish Game* 60(1):26-35.
- Gall, G. A. E., and S. J. Gross. 1978. A genetics analysis of the performance of three rainbow trout broodstocks. *Aquaculture* 15:113-127.
- Gandolfi, G. 1971. Sexual selection in relation to the social status of males in Poecilia reticulata (Teleostei: Poeciliidae) *Boll. Zool.* 38(1):35-48.
- Gilbert, C. H. 1923. The salmon of the Yukon River. *Bull. U.S. Bur. Fish.* 38:317-332.
- Goryczko, K., and L. Tomasik. 1975. An influence of males on the viability and fertilization degree of trout eggs. *Acta Ichthyologica et Piscatoria* 5(1):3-11.

- Grant, B., G. A. Snyder, and S. F. Glessner. 1974. Frequency-dependent mate selection in Mormoniella vitripennis. *Evolution* 28(2):259-264.
- Gray, J. 1928. The growth of fish. II. The growth rate of the embryo of Salmo fario. *Br. J. Exp. Biol.* 6:110-124.
- Gray, P. L. 1965. Fecundity of the chinook salmon (Oncorhynchus tshawytscha) related to size, age, and egg diameter. M.S. Thesis, Univ. Washington, Seattle. 65 pp.
- Graybill, J. P. 1978. Role of depth and velocity for nest site selection by Skagit River pink and chum salmon. 1978 Northeast Pacific Pink and Chum Salmon Workshop. Pac. Biol. Sta., Nanaimo, B.C.
Pages 391-392.
- Hanson, A. J., and H. D. Smith. 1967. Mate selection in a population of sockeye salmon (Oncorhynchus nerka) of mixed age-groups. *J. Fish. Res. Board Can.* 24(9):1955-1977.
- Hawke, S. P. 1978. Stranded redds of quinnat salmon in the Mathias River, South Island, New Zealand. *N.Z. J. Mar. Freshwater Res.* 12(2):167-171.
- Heard, W. R. 1972. Spawning behavior of pink salmon on an artificial redd. *Trans. Amer. Fish. Soc.* 101(2):276-283.
- Helle, J. H. 1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, Oncorhynchus keta

- (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Ph.D. Dissertation, Oregon State Univ., Corvallis. 118 pp.
- Hoopes, D. T. 1972. Selection of spawning sites by sockeye salmon in small streams. Fish. Bull. 70(2):447-458.
- Hopley, C. W., Jr. 1975. The effect of parental age-class on the early life history of hatchery-reared chinook salmon (Oncorhynchus tshawytscha). M.S. Thesis, Univ. Washington, Seattle. 55 pp.
- Houston, A. H. 1961. Influence of size upon the adaptation of steelhead trout (Salmo gairdneri) and chum salmon (Oncorhynchus keta) to seawater. J. Fish. Res. Board Can. 18(3):401-415.
- Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbeiana. Evolution 32(4):850-871.
- Hublou, W. F. 1963. Oregon pellets. Prog. Fish Cult. 25:175-180.
- Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.
- Huxley, J. S. 1923. Late fertilization and sex ratio in trout. Science 58:291-292.
- Huxley, J. S. 1934. A natural experiment on the territorial instinct. British Birds 24(10):270-277.
- Huxley, J. S. 1938. The present standing of the theory of sexual selection. Pages 11-42 in G. R. de Beer, ed. Evolution: essays on

aspects of evolutionary biology presented to Professor E. S. Goodrich on his seventieth birthday. Clarendon Press, Oxford.

Ihssen, P. 1976. Selective breeding and hybridization in fisheries management. J. Fish. Res. Board Can. 33(2):316-321.

Ivankov, V. N., and V. L. Andreyev. 1969. Fecundity of Pacific salmon (Genus Oncorhynchus spp.). Problems of Ichthyology 9(1):59-66.

Jehl, J. R., Jr. 1970. Sexual selection for size differences in two species of sandpipers. Evolution 24(2):311-319.

Jensen, P. T., and J. Hyde. 1971. Sex ratios and survival estimates among salmon populations. Cal. Fish Game 57(2):90-98.

Jones, J. W., and J. N. Ball. 1954. The spawning behavior of brown trout and salmon. Brit. J. Ani. Behav. 2:103-114.

Jones, J. W., and G. M. King. 1950. Progeny of male salmon parr. Salmon and Trout Magazine 128:24-26.

Jones, J. W., and G. M. King. 1952. The spawning of the male salmon parr (Salmo salar Linn. juv.). Proc. Zool. Soc. London 122:615-619.

Kanid'ev, A. N. 1966. Tolerance of hatchery-reared juvenile keta (Oncorhynchus keta) to rate of flow and to predaceous fishes. Tr. Murmansk. Morsk. Biol. Inst. 12. 16:101-111. Biol. Abst. No. 114637, 1968.

- Kato, T. 1978. Relation of growth to maturity of age and egg characteristics in kokanee salmon (Oncorhynchus nerka). Bull. Freshwater Fish. Res. Lab. Tokyo 28(1):61-75.
- Kodric-Brown, A. K. 1977. Reproductive success and the evolution of breeding territories in pupfish (Cyprinodon). Evolution 31:750-766.
- Koo, T. S. Y. 1962. Age designation in salmon. Pages 37-48 in T. S. Y. Koo, ed. Studies of Alaska Red Salmon, Vol. I. Univ. Washington Press, Seattle.
- Koski, K V. 1975. The survival and fitness of two stocks of chum salmon (Oncorhynchus keta) from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Ph.D. Dissertation Univ. Washington, Seattle. 212 pp.
- Kuznetsov, I. I. 1928. Some observations on spawning of the Amur and Kamchatka salmons. Izy. Tikhookeanskoi Nauchno-promyslovoi Stanstii 2(3):1-195. [Fish. Res. Board Can. Transl. Ser. No. 22.]
- Lannan, J. E. 1976. Possibilities for genetic programs in ocean ranching. Pages 25-32 in T. Nosho and W. K. Hershberger, eds. Salmonid genetics: status and role in aquaculture. Univ. Washington, Sea Grant Rep. WSG W0-76-2.
- Larsson, P., and J. Pickova. 1978. Egg size of salmon (Salmo salar L.) in correlation to female age and weight in three river stocks. Laxforskningsinstitute Meddelande 1978:2. 6 pp.

- Leitritz, E. 1959. Trout and salmon culture. Cal. Dep. Fish Game Fish. Bull. 107:1-169.
- Levanidov, V. Ya. 1964. On the relationship between the size of fingerling Amur autumn chum Oncorhynchus keta infrasp. Autumnalis Berg, and their survival. Voprosy Ikhtiologii. 4(4):658-663. Biol. Abst. N. 10704. 1966.
- Licht, L. E. 1976. Sexual selection in toads (Bufo americanus). Can. J. Zool. 54:1277-1284.
- Lill, A. 1968a. An analysis of sexual isolation in the domestic fowl: I. The basis of homogamy in males. Behaviour 30:107-126.
- Lill, A. 1968b. An analysis of sexual isolation in the domestic fowl: II. The basis of homogamy in females. Behaviour 30:127-145.
- Lister, D. B., and C. E. Walker. 1966. The effect of flow control on freshwater survival of chum, coho, and chinook salmon in the Big Qualicum River. Can. Fish. Cult. 37:3-25.
- Lowther, J. K. 1961. Polymorphism in the white-throated sparrow, Zonotrichia albicollis (Gmelin). Can. J. Zool. 39:281-292.
- Mahon, E. F., and W. S. Hoar. 1956. The early development of the chum salmon, Oncorhynchus keta (Walbaum). J. Morphology 98(1):1-47.
- Mathisen, O. A. 1955. Studies on the spawning biology of the red salmon Oncorhynchus nerka (Walbaum) in Bristol Bay, Alaska with

- special reference to the effect of altered sex ratios. Ph.D. Dissertation, Univ. Washington, Seattle. 285 pp.
- Mathisen, O. A. 1962. The effect of altered sex ratios on the spawning of red salmon. Pages 137-245 in T. S. Y. Koo, ed. Studies of Alaska red salmon, Vol. I. Univ. Washington Press, Seattle.
- Mattson, C. R., and R. G. Rowland. 1963. Chum salmon studies at Traitors Cove Field station June 1960 to March 1963. Bur. Commer. Fish., Biol. Lab. Auke Bay, Alaska, Rep. 63-11. 32 pp.
- Mattson, C. R., R. G. Rowland, and R. A. Hobart. 1964. Chum salmon studies in southeastern Alaska. Bur. Commer. Fish., Biol. Lab. Auke Bay, Alaska. M.S. Rep. 64-8. 22 pp.
- May, B. 1975. Electrophoretic variation in the genus Oncorhynchus: the methodology, genetic basis, and practical applications to fisheries research and management. M.S. Thesis, Univ. Washington, Seattle. 95 pp.
- May, B., F. M. Utter, and F. W. Allendorf. 1975. Biochemical genetic variation in pink and chum salmon: Inheritance of intraspecies variations and apparent absence of interspecies introgression following massive hybridization of hatchery stocks. J. Hered. 66(4):227-232.
- Maynard Smith, J. 1978. The evolution of sex. Cambridge Univ. Press, Cambridge. 222 pp.

- Mayr, E. 1976. Evolution and the diversity of life: selected essays. Belknap Press of Harvard Univ. Press, Cambridge, MA. 721 pp.
- McCart, P. 1969. Digging behavior of Oncorhynchus nerka spawning in streams at Babine Lake, British Columbia. Pages 39-51 in T. G. Northcote, ed. Symp. on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Inst. Fish. Vancouver.
- McCart, P. 1970. A polymorphic population of Oncorhynchus nerka at Babine Lake, B.C. involving anadromous (sockeye) and nonanadromous kokanee forms. Ph.D. Dissertation, Univ. British Columbia, Vancouver. 135 pp.
- McCracken, G. F., and J. W. Bradbury. 1977. Paternity and genetic heterogeneity in the polygynous bat, Phyllostomus hastatus. Science 198(4314):303-306.
- McNeil, W. J. 1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of Southeastern Alaska. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 402. 15 pp.
- McNeil, W. J., and J. E. Bailey. 1975. Salmon rancher's manual. Northwest Fish. Center Auke Bay. Fish. Lab. Processed Rep. 95 pp.
- Neave, F. 1966. Salmon of the North Pacific Ocean-part III. A review of the life history of North Pacific salmon 6. Chum salmon in British Columbia. Int. North Pac. Fish. Comm. Bull. 18:81-85.

- Nelson, K., and D. Hedgecock. 1977. Electrophoretic evidence of multiple paternity in the lobster Homarus americanus (Milne-Edwards). Amer. Natural. 11(978):361-365.
- Newcombe, L., and G. Hartman. 1973. Some chemical signals in the spawning behavior of rainbow trout (Salmo gairdneri). J. Fish. Res. Board Can. 30:995-997.
- Noble, G. K. 1938. Sexual selection among fishes. Biol. Rev. 13:133-158.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Natural. 103(934):589-603.
- Painter, R. E. 1962. Relationship of fish length and mate selection in the sockeye salmon, Oncorhynchus nerka (Walbaum). M.S. Thesis, Univ. Michigan, Ann Arbor. 32 pp.
- Parker, R. R. 1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Board Can. 20(6):1441-1455.
- Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757-794.
- Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503-1510.

- Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 18:1503-1510.
- Parsons, P. A. 1965. Assortative mating for a metrical characteristic in Drosophila. Heredity 20(2):161-167.
- Parsons, P. A. 1967. Behavior and random mating. Experientia 23(7):585-586.
- Perrone, M., Jr. 1978. Mate size and breeding success in a monogamous cichlid fish. Environ. Biol. Fish. 3(2):193-201.
- Petit, C., and L. Ehrman. 1969. Sexual selection in Drosophila. Evol. Biol. 3:177-223.
- Poon, D. C. 1977. Quality of salmon fry from gravel incubators. N.W. Alaska Fish. Ctr. Processed Rep. U.S. Dep. Com., NOAA, NMFS. 253 pp.
- Potter, D. A., D. L. Wensch, and D. E. Johnston. 1976. Guarding, aggressive behavior, and mating success in male twospotted spider mites. Annu. Entomol. Soc. Am. 69(4):707-711.
- Potter, D. A., D. L. Wensch, and D. E. Johnston. 1976. Aggression and mating success in male spider mites. Science 193(4248):160-161.

- Pratt, J. D. 1968. Spawning distribution of Atlantic salmon (Salmo salar L.) in controlled flow channels. M.S. Thesis, Memorial Univ. Newfoundland. St. John's. 143 pp.
- Pritchard, A. L. 1937. Variation in the time of run, sex proportions, size and egg content of adult pink salmon (Oncorhynchus gorbuscha) at McClinton Creek, Masset Inlet, B.C. J. Biol. Board Can. 3(5):403-416.
- Privol'nev, T. I., Z. I. Galkina, and G. G. Galkin. 1964a. How the size of female salmon and their eggs affects the progeny. Pages 160-168 in T. I. Privol'nev, Fish physiology in acclimatization and breeding. Bull. of the State Sci. Inst. of Lake and River Fisheries Vol. 58. [Transl. by Israel Programs for Sci. Transl., Jerusalem, 1970.]
- Privol'nev, T. I., Z. I. Galkina, and G. G. Galkin. 1964b. Heterogeneity of mature eggs of salmon (Salmo salar L.) and of bream (Abramis brama L.). Pages 151-159 in T. I. Privol'nev, Fish physiology in acclimatization and breeding. Bull. Sci. Inst. of Lake and River Fisheries Vol. 58. [Transl. Israel Programs for Sci. Transl., Jerusalem, 1970.]
- Ralls, K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. Amer. Natural. 111(981):917-938.

- Reimers, P. E. 1978. Measuring long-term changes in the fall chinook population in Elk River. Oregon Dep. Fish Wildl. Info. Rep. Ser. Fish. No. 78-5.
- Ricker, W. E. 1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Board Can. 21(5):905-931.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27-160 in R. C. Simon and P. A. Larkin, eds. The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.
- Ricker, W. E., H. T. Bilton, and K. V. Aro. 1978. Causes of the decrease in size of pink salmon (Oncorhynchus gorbuscha). Fish. Mar. Ser. Tech. Rep. 820. 93 pp.
- Rohwer, S., S. D. Fretwell, and D. M. Niles. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Amer. Natural. 115(3):400-437.
- Ross, M. R., and R. J. Reed. 1978. The reproductive behavior of the fallfish (Semotilus corporalis). Copeia 1978(2):215-221.
- Rounsefell, G. A. 1957. Fecundity of North American Salmonidae. U.S. Fish. Wildl. Serv. Fish. Bull. 57(122):451-468.

- Sano, S. 1966. Salmon of the North Pacific Ocean-part III. A review of the life history of North Pacific salmon 3; chum salmon in the Far East. Inst. North Pac. Fish. Comm. Bull. 18:41-57.
- Sato, R. 1972. Studies on the survival of downstream chum salmon fry which were released after feeding in a freshwater pond. Pages 67-76 in J. E. Bailey, ed. Proceedings of the 1972 Northeast Pacific Pink and Chum Salmon Workshop. Informational leaflet No. 161, ADF&G.
- Schroder, S. L. 1973. Effects of density on the spawning success of chum salmon (Oncorhynchus keta) in an artificial spawning channel. M.S. Thesis, Univ. Washington, Seattle. 78 pp.
- Schroder, S. L. 1975. Assessment of production of chum salmon fry from the Big Beef Creek spawning channel. Annu. Rep. Anadromous Fish Project AFC-67. Fish. Res. Inst. Univ. Washington, FRI-UW-7513. 53 pp.
- Schroder, S. L. 1977. Assessment of production of chum salmon fry from the Big Beef Creek spawning channel. Completion Rep. Anadromous Fish Project AFC-67. Fish. Res. Inst., Univ. Washington, FRI-UW-7718. 77 pp.
- Schultz, L. P., and students. 1935. The breeding activities of the little redbfish, a landlocked form of the sockeye salmon, Oncorhynchus nerka. Pan-Pacific Res. Inst., Honolulu 10(1):67-77.

- Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (Agelaius phoeniceus). Amer. Natural. 114(1):77-100.
- Seeb, J., and L. Wishard. 1977. The use of biochemical genetics in the management of Pacific salmon stocks: genetic marking and mixed fishery analysis. Final Rep. Wash. Dep. Fish. Serv. Contr. No. 792.
- Selander, R. K. 1965. On mating systems and sexual selection. Amer. Natural. 99(906):129-141.
- Shapovalov, L., and A. C. Taft. 1954. The life histories of the steel-head rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations regarding their management. Cal. Dep. Fish Game Fish. Bull. 98. 375 pp.
- Sheppard, P. M. 1952. A note on the nonrandom mating in the moth, Panaxia dominula. Heredity 6:239-241.
- Sibert, J. 1972. A model of juvenile pink salmon growth in the estuary. Pages 25-39 in J. E. Bailey, ed. Proc. 1972 Northeast Pacific Pink and Chum Salmon Workshop. Informational Leaflet No. 161. ADF&G.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York. 312 pp.

- Sinnock, P. 1970. Frequency dependence and mating behavior in Tri-bolium castaneum. Amer. Natural. 104(939):469-476.
- Smirnov, A. I. 1955. The effect of mechanical agitation at different periods of development on the eggs of autumn chum salmon (Oncorhynchus keta infra sp. autumnalis Berg, Salmonidae). Zoologicheskii Zhurnal Akademiia Nauk SSR 38(5):734-744. [Transl. Fish. Res. Board Can. Transl. Ser. No. 230.]
- Smirnov, A. I. 1975. The biology, reproduction, and development of the Pacific salmon. Izd. Mosk. Univ., 335 pp. [Fish. Mar. Serv. Transl. Serv. No. 3861. Pac. Biol. Sta., Nanaimo, B.C. 1976.]
- Smith, E. V. 1916. Effect of light on the development of young salmon. Puget Sound Mar. Sta. Publ. 1(11):89-107.
- Smolei, A. I. 1966. Fecundity of sevan trouts. Vop. Ikhtiolo. 6(1):77-83. [Biol. Abstr. No. 11481, Vol. 49, 1968.]
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 pp.
- Spiess, R. 1968. Low frequency advantage in mating of Drosophila pseudoobscura karyotypes. Amer. Natural. 102(926):363-379.
- Stacey, P. B., and D. Chiszar. 1978. Body color pattern and the aggressive behavior of male pumpkinseed sunfish (Lepomis gibbosus) during the reproductive season. Behaviour 64(3-4):241-297.

- Tautz, A. F., and C. Groot. 1975. Spawning behavior of chum salmon (Oncorhynchus keta) and rainbow trout (Salmo gairdneri). J. Fish. Res. Board Can. 32(5):633-642.
- Taylor, C. E. 1975. Differences in mating propensities: some models for examining the genetic consequences. Behav. Gen. 5(4):381-393.
- Thornhill, R. 1979. Adaptive female-mimicking behavior in a scorpion-fly. Science 205:412-414.
- Thorpe, J. E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (Salmo salar L.) under artificial rearing conditions. J. Fish. Biol. 11:175-184.
- Thorpe, J. E., and R. I. G. Morgan. 1978. Parental influence on growth rate, smolting rate and survival in hatchery reared juvenile Atlantic salmon, Salmo salar. J. Fish. Biol. 13:549-556.
- Tilley, S. G., and J. S. Hausman. 1976. Allozymic variation and occurrence of multiple inseminations in populations of the salamander Desmognathus ochrophaeus. Copeia 1976(4):734-741.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, ed. Sexual selection and the descent of man 1871-1971. Aldin Publ. Co., Chicago.
- Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 30:253-269.

- Utter, F. M., H. O. Hodgins, and F. W. Allendorf. 1974. Biochemical genetic studies of fishes: potentialities and limitations. Pages 213-238 in D. C. Malins and J. R. Sargent, eds. Biochemical and biophysical perspectives in marine biology, Vol. 1. Acad. Press, London and New York.
- Velsen, F. P. J. 1980. Embryonic development in eggs of sockeye salmon, Oncorhynchus nerka. Canadian Special Publ. Fish. Aqua. Sci. 49. 19 pp.
- Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18:252-261.
- Verner, J., and M. F. Willson. 1966. The influence of habitats on mating systems of North American Birds. Ecology 47:143-147.
- Vladimirov, V. I. 1973. The effect of the growth rate of spawners on the survival and abundance of the progeny. J. Ichthyology 13(6):801-812.
- Walker, J. H. C. 1974. Mechanics of size selected predation by coho smolts on pink and chum salmon fry. Pages 114-120 in D. R. Harding, ed. Proc. 1974 Northeast Pacific Pink and Chum Salmon Workshop. Dep. Environ. Fish. Canada.
- Wallace, B. 1968. Topics in population genetics. W. W. Norton and Co. Inc., New York. 481 pp.

- Welch, P. S. 1948. Limnological methods. Blakiston, Philadelphia
381 pp.
- Wickett, W. P. 1952. Production of chum and pink salmon in a controlled stream. Fish. Res. Board Can., Pac. Prog. Rep. 93:7-9.
- Wilbur, H. M., D. I. Rubenstein, and L. Fairchild. 1978. Sexual selection in toads: the roles of female choice and male body size. *Evolution* 32(2):264-270.
- Williams, G. C. 1975. Sex and evolution. Princeton Univ. Press, Princeton. 200 pp.
- Wilson, E. O. 1975. Sociobiology: the new synthesis. The Belknap Press of Harvard Univ. Press, Cambridge, MA. 697 pp.
- Yanai, J., and G. E. McClearn. 1972. Assortative mating in mice. I. Female mating preference. *Behav. Genet.* 2:173-183.
- Yanai, J., and G. E. McClearn. 1973a. Assortative mating in mice II. Strain differences in female mating preference, male preference, and the question of possible sexual selection. *Behav. Genet.* 3(1):65-74.
- Yanai, J., and G. E. McClearn. 1973b. Assortative mating in mice III. Genetic determination of female preference. *Behav. Genet.* 3(1):75-84.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall Inc.,
Englewood Cliffs, NJ. 620 pp.

APPENDIX I: THE METHOD USED TO CALCULATE THE EXPECTED PAIRINGS AMONG FISH PLACED INTO THE EXPERIMENTAL STREAM

The following example will illustrate how expected pairings among fish placed into each section of the experimental stream were calculated. Suppose that a section contains five males and five females with the following body weights:

FEMALES		MALES	
Tag no.	Weight (kilograms)	Tag no.	Weight (kilograms)
1	3.0	1	2.0
2	3.0	2	4.0
3	2.0	3	5.0
4	2.0	4	3.0
5	3.0	5	1.0

If mating occurred randomly, every male would have an equal probability of pairing with every female and thus there would be 25 possible combinations of males and females (i.e., 5 00 x 5 00). Each possible combination has a male body weight:female body weight size ratio. The probability of a pair forming with a particular size ratio can be calculated by: 1) transforming every possible size ratio into a quotient (e.g., the five quotients for male one equal 0.66 for females one, two, and five, and 1.0 for females three and four); 2) placing each quotient into an

arbitrary class (for male one, 0.66 or 1.0), and 3) dividing the number of pairs falling into each class by the number of possible male-female combinations (in this case 25). If 150 pairs had been observed in this section the expected number falling into each arbitrary class would equal its probability of occurrence multiplied by 150. The results of such a mathematical treatment on this hypothetical population are illustrated below:

The expected number of paris falling into various classes after 150 pairs had been observed

Class	0.33	0.50	0.66	1.00	1.33	1.50	1.66	2.00	2.50
Sum of the pairs falling into each class	3	2	3	5	3	2	3	2	2
Probability	0.12	0.08	0.12	0.20	0.12	0.08	0.12	0.08	0.08
Expected no. of pairs (out of 150)	18	12	18	30	18	12	18	12	12

In the above example, I assumed that all the fish were sexually active and therefore theoretically available to each memeber of the opposite sex. In a few sections some individuals were not sexually active during every observation period. The expected number of pairs falling into each class can be modified to account for this by calculating additional probability sets. For example, assume that male "one" did not become sexually active until after 50 pairs had been observed. The first set of probabilities would exclude him while a second set would be identical to the probabilities shown above. The expected

values would be calculated as before, except that the first set of probabilities should be multiplied by 50 and the second by 100. By summing the obtained values the overall expected value of each class can then be determined.

VITA

Steven Lee Schroder, son of William L. Schroder and Marjorie Lee, was born in Seattle, Washington, on September 5, 1945. He graduated from Roosevelt High School in Seattle in 1963, and enrolled in Olympic College, Bremerton, Washington, the following fall. While at Olympic College he majored in Botany. In 1965 he transferred to the University of Washington where in 1969, he received his Bachelor of Science Degree in Fisheries Science. He began working at the University of Washington's Big Beef Creek Fish Research Station as a technician in 1970. He was admitted into the University of Washington's Graduate School in 1971, and received his Master of Science Degree in 1973. During 1972 and 1973 he spent several months in Panama working as a fisheries consultant. Once he returned from Panama, he was awarded a Pre-doctoral Research Assistantship with the Fisheries Research Institute and served as a project leader on some of the chum salmon investigations which took place at Big Beef Creek. Since May 1981 he has worked for the Washington State Department of Fish as a fisheries research scientist.

He married Kate P. Folkins in Seattle, Washington, on May 10, 1974. They have a daughter Heidi, and currently reside in Seabeck, Washington. Professional organizations to which he belongs include the American Institute of Fisheries Research Biologists, Sigma Xi, and Pacific Fishery Biologists.