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ASSESSMENT OF PRODUCTION OF CHUM SALMON FRY FROM THE BIG BEEF CREEK SPAWNING CHANNEL

Annual Report - Anadromous Fish Project

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PREFACE

The philosophy or intent of the research program at the Big Beef Creek Fish Research Station is to design and evaluate various management strategies for chum salmon that will have practical application in spawning channels, hatcheries, ocean ranches, and natural stream systems. The approach used in evaluating these programs is one of observing the behavioristic and physiological responses of chum salmon adults, fry, and embryos under a variety of controlled situations.

Sumner (1939), as quoted by Foerster (1968), aptly encapsulated this philosophy by writing: "Unfortunately, we are unable to put questions, or at least verbal ones, to our fishes with any reasonable expectation of receiving replies. But the animals are nonetheless able to inform us to a certain extent regarding their sense impressions....A fish' replies to our questions are given in physiological or behavioristic terms.... It is common sense, rather than scientific experiment, which leads us to believe that the fish is not a mere unconscious mechanism."

Obviously, if our attempts to increase salmon populations are to succeed, we must have knowledge of the biological requirements of the stocks we wish to enhance. Clearly, the more we know about salmon populations, the more refined and successful our attempts will be in their proliferation. The past (Koski, 1975; Schroder, 1975; and Beall, 1972) and present role of the Big Beef Creek station is one of applied research--a testing arena designed to allow investigators to enrich our knowledge about these intrinsically fascinating and economically important fish.

This second of three reports deals entirely with recent results obtained at Big Beef Creek which deal with mate selection patterns found in chum salmon. Preliminary analyses of data gathered during the past year indicate that this species mates predominantly in an assortative fashion. The biological factors that may be responsible for such a non-random mating scheme are explored and tentative speculations regarding its origins are offered.

The third and final report will summarize the results of the following studies that have been conducted at Big Beef Creek during the past 3 years:

1. the effects of redd superimposition on the survival and quality of chum salmon fry produced from a spawning channel,
2. the effects of different gravel depths over sand substrates on the survival and quality of chum salmon fry, and
3. an examination of the proximate and ultimate factors responsible for the assortative mating system which apparently exists in chum salmon.

In addition, the Final Report will also include a section describing the contributions of our experimental channels to the commercial chum salmon fishery during the past 3 years.

Crow and Kimura, 1970).

Clearly, an organism is composed of a unity of genetic traits, not all of which influence the phenotypic characters used in mate selection. Thus, it is quite possible for a species to mate randomly for one genetic trait and non-randomly for another (Wallace, 1968). Hence, any study that investigates mate selection must define the genetic traits (morphological, behavioral, and/or physiological) in the mating pairs that are being used to determine the observable patterns.

A study on the mate selection patterns found in sockeye salmon (O. nerka) determined that individuals of similar lengths tended to pair with one another (Hansen and Smith, 1967). In this species, there is a strong correlation between age and size at maturity; therefore, the observed mating pattern allowed similarly-aged fish to pair with one another more often than if mating were entirely random. A comparable correlation between age and size at maturity exists in chum salmon. Consequently, experiments were developed to test whether a similar pattern of mate selection existed in this species.

The purpose of the present study is broadly two-fold:

1. to determine if chum salmon of similar body weights and hence, age have a tendency to pair with one another, and
2. to attempt to rationalize the observable patterns of mate selection on the basis of fitness--as it relates to both the spawning adults and progeny produced from various types of matings.

In attempting to fulfill these objectives, various types of observations were conducted on spawning adults, developing embryos,

INTRODUCTION

There are obvious advantages in understanding how gene exchange occurs in populations of chum salmon (*Oncorhynchus keta*). By discovering the processes by which mates are selected and the underlying biological factors responsible for such selection, managers of this species will be given practical biological information with direct applicability in artificial breeding programs, i.e., those that might be implemented in hatcheries or "ocean ranches". Furthermore, by examining how alterations in sex ratio and density of spawners may influence mating patterns, the information has even broader appeal, e.g., to biologists concerned with maintaining wild or quasi-wild stocks in rivers or spawning channels.

The importance of understanding the processes involved in mate selection lies in the premise that it may be indirectly responsible for altering the gene frequencies within a population (micro-evolution). The selection of mates cannot, per se, alter the frequency of a set of genes, but it may alter the frequencies of the genotypes that will be subjected to natural selection. Obviously, natural selection can differentially select or favor those genotypes with the highest viability. Consequently, shifts in gene frequencies can happen if a differential survival rate occurs among the produced genotypes (Mayr, 1963; Crow and Kimura, 1970; and Wilson, 1975).

In general, chum salmon may select their mates randomly or in an assortative fashion. In assortative mating, the paired individuals may be more similar (positive assortative or assortative mating), or less similar (negative assortative or disassortative mating) on the average than mating pairs chosen by some random process (Wallace, 1968; and

and the growth patterns of propagules produced from selected artificial crosses. A portion of the study was also concerned with examining differences in the number, size, and nutritive properties of eggs originating from differently-aged females. Additionally, a small experiment examined possible differences in the percentage of water present in milt produced from individual males throughout their spawning lifetimes.

METHODS AND MATERIALS

Experimental Fish

Chum salmon originating from Big Beef Creek which flows into the east shore of Hood Canal (Kitsap County, Washington State) were used. Migrating chum salmon enter this stream from mid-September through January, with peaks of abundance occurring in early October (early run), mid-November (middle run), and late December (late run). The majority of the returning adults are four (60-80%) or three (20-40%) years old, with very few returning at five (1-5%) and even less at two (0.0-0.5%) years of age. Generally, 4- and 5-year-old fish are similar in size at maturity and larger than mature 3-year-olds which, in turn, are larger than 2-year-old adults (Schroder, 1973; and Koski, 1975).

As the fish migrate into the stream, they are captured in one of two traps and processed in a manner previously described by Schroder (1973) and Koski (1975). Each fish used in the mate selection studies was examined for maturity, anesthetized in MS-222 (tricaine methanesulfonate), weighed, measured, aged, tagged with large Petersen discs, and trucked 400 m or less to designated portions of a spawning channel located on a side branch of Big Beef Creek.

Spawning Channel

Five 3.5-m x 15.2-m sections of a spawning channel were used to examine mate selection patterns under various spawner densities and sex ratio regimes. Each section of the channel had a 0.25% gradient (.25 m/100 m), was filled with 75 cm of coarse (.8 cm - 6.25 cm) stream gravel, and was equipped with a 3-m high observation wall supplied with viewing ports. Water velocity was kept at 22.5 cm/sec and depth at 30 cm throughout the experiments. Occasionally high tides influenced some of the lower sections of the channel, reducing velocity to zero and increasing water depth to 1 m or more. These alterations did not last for more than several hours, nor did they appear to disturb the experimental fish. During the experiments, the surface water temperatures ranged from 13.9 C to 5.6 C, and dissolved oxygen concentrations as determined by a YSl Model 54 oxygen meter were near saturation at all times. Further details concerning the construction, design, and additional experimental uses of the channel can be found in Beall (1972), Schroder (1973), and Koski (1975).

Observation of Fish in the Spawning Channel

Observations were made only during daylight hours and were primarily concerned with determining the reproductive status of both males and females in each experimental section of the channel. Notations were made hourly concerning the size ratios of pairs and the color patterns present on "alpha" (courting), "satellite" (subdominant courting), and "non-courting" males. Since each fish had an identifying set of tags, it was possible to determine the size ratio and ages for each mating pair observed.

A variety of sex ratio and spawner density regimes was examined. Two sections of the channel had 1:1 sex ratios and identical spawner densities of 30 ♀♀ or 1.55 m^2/♀. Two others had similar sex ratios (2 ♂♂:1 ♀) but slightly different spawner densities (13 ♀♀ or 3.58 m^2/♀ and 14 ♀♀, or 3.32 m^2/♀). The last section had a sex ratio of .75 ♂:1 ♀ and the eight females in this section were allocated 5.81 m^2 of spawning substrate each.

Viewing Chamber Observations of Single Pairs of Spawning Fish

Eleven pairs of spawning fish were observed one at a time in a viewing chamber located at the inlet of the spawning channel. The chamber consists of two parts, a concrete observation well (1.8 m x 3.3 m x 2.4 m) that was provided with both horizontal (1-m x 1-m) and vertical (1-m x 1.5-m) windows and a 3.5-m x 3.5-m gravel bed (Fig. 1).

The video tape system used to record observations included a Sanyo Video Tape Recorder Model 1200, Panasonic "Nighthawk" camera Model WV-260P, and a Setchell Carlson 10-inch monochrome video monitor Model 10M915. While operating in its slow motion mode, the Sanyo VTR can record 12 continuous hours of observations/roll of video tape. The Panasonic camera had two interchangeable lenses, an f/1.8, 12.5-mm - 75-mm zoom and an f/1.5, 8.5-mm wide angle lens. The camera came equipped with a separate mesh silicon vidicon and is capable of operating with as little illumination as 0.1 ft-candle. The combination of this equipment allowed continuous filming from early morning through dusk.

Video tape records were made of the behavioral interactions that occurred between paired fish representing various size ratio classes.

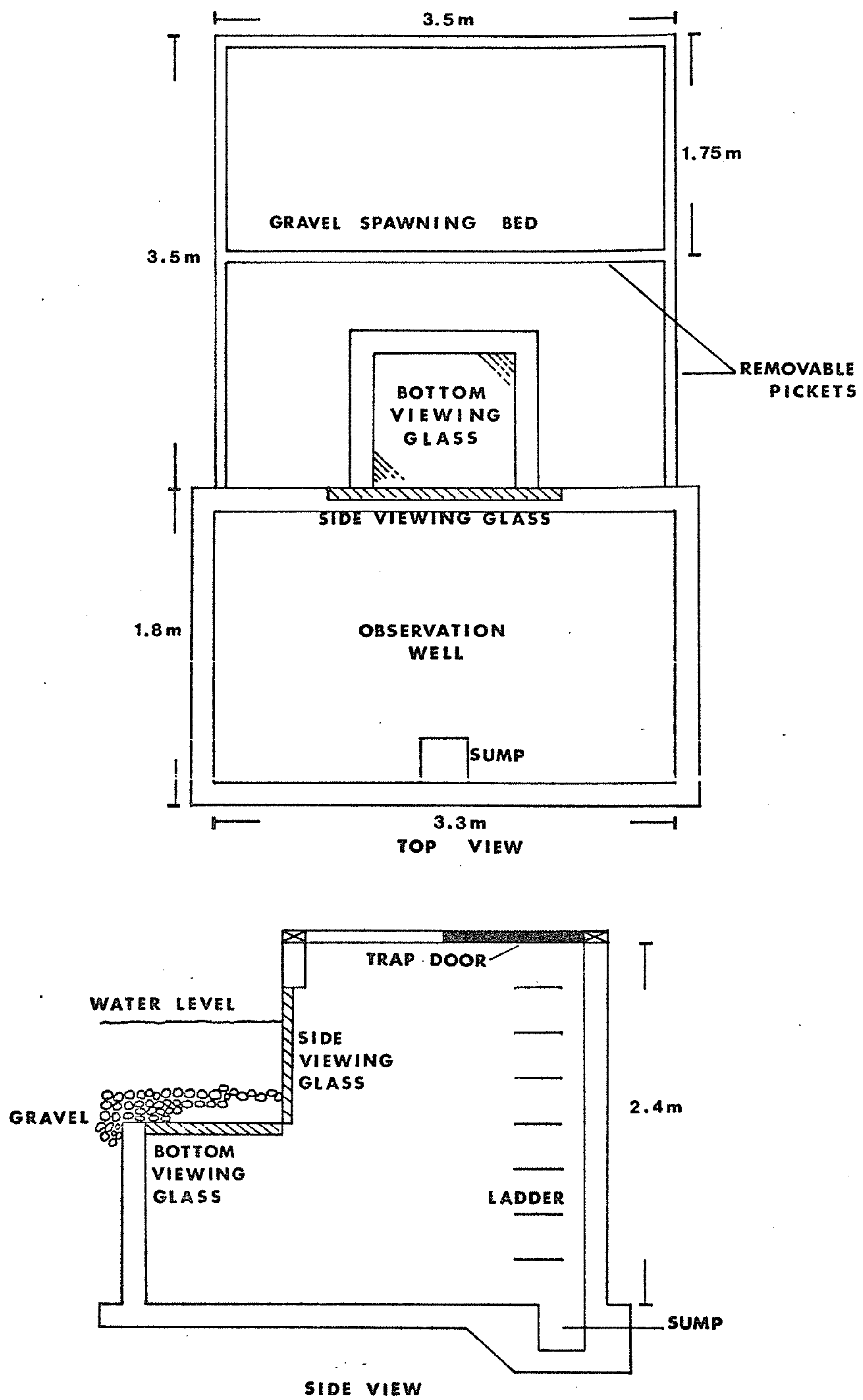


FIG. 1. Top and side views of the viewing chamber used to house videoptape equipment employed in producing behavioral records of spawning chum salmon.

The four size classes (0.5:1, 1.1:1, 2:1, and 3.5:1) examined were based upon the ratios that existed between the body weight (♂ body weight: ♀ body weight) of the members of each pair.

While pairs were being filmed, the gravel bed surrounding the observation well was subdivided by a longitudinal picket into two 1.75-m x 3.5-m sections. Twelve hr prior to filming, a male and female were introduced into separate portions of the divided gravel bed. At the onset of filming, the female was removed from her section and placed with the male in the gravel section adjacent to the observation windows. The video equipment was then turned on and the fish were allowed to spawn two, and often three, times before they were removed.

The water velocity in the chamber was initially 22.5 cm/sec but was altered by each female as she started to construct her redd. Water temperatures varied from 5.6 C to 8.9 C, depth was kept at 35 cm, and the gravel substrate was raked level prior to the introduction of each pair of fish.

Egg characteristics of 3- and 4-year old Chum Salmon

Two hundred and twenty-one females (forty-seven 3-year olds and one hundred seventy-four 4-year-olds) were used to examine the characteristics of eggs produced from 3- and 4-year old fish originating from the middle run of Big Beef Creek. The entire egg complement of each female was removed and weighed to the nearest g on a Chatillon 6-k x 10-g balance. After the eggs were weighed, a sample of 60 to 200 eggs was withdrawn and weighed on a Mettler P 1200 balance to the nearest 0.01 g. These two weights were used in the following algebraic formula to estimate the fecundity of each female:

$$\text{fecundity} = \frac{(\text{no. of eggs/sample})(\text{total egg wt})}{(\text{wt of the sample})}$$

The eggs from each sample were allowed to water harden for 12 hours before they were measured and weighed. Three subsamples of 20 eggs from each sample were measured to the nearest .5 mm on a board held by a stand at a 25-degree angle. Every subsample of measured eggs was blotted dry and weighed to the nearest .01 g on a Mettler P 120 balance. The eggs were then placed in a Precision Thelco Model 17 drying oven and baked for 24 hours at 97 C. After drying, the eggs were placed in a vacuum dessicator supplied with anhydrous calcium chloride and allowed to cool before they were reweighed on the Mettler P 120 balance.

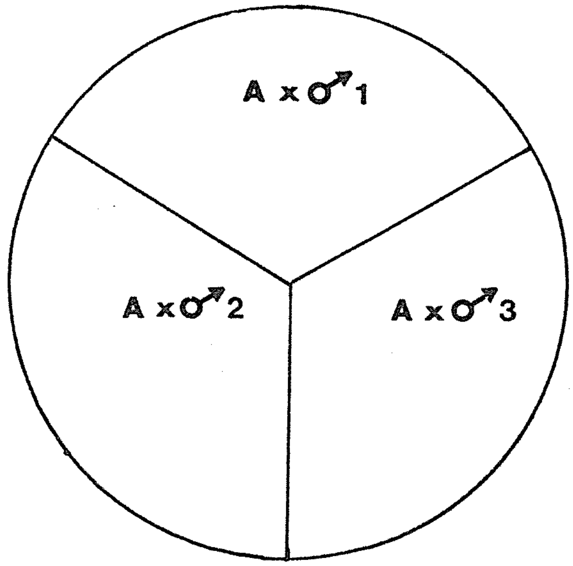
Fish Culture

To examine the possible effects of parental age and size on the developmental rates and growth patterns in alevins and fry, two sets of controlled breeding experiments were performed. In both experiments, the female parents were anesthetized in MS-222, had their caudal peduncles severed, and were bled thoroughly before any eggs were removed. Milt from selected males was added to the eggs and the spawn was then transported approximately 1/2 mile from the research station to an artesian water source. The eggs were fertilized at this location just prior to their placement into standard Heath incubator trays. After the eggs had reached the "eyed stage" of development, they were "shocked" and mortalities from each cross were removed. The remaining live eggs were returned to Heath trays which had been modified by the attachment of an Astroturf substrate to the bottom screen. A flow of 11 liters/min was maintained in each Heath tray and the water temperature ranged from 8.7 C to 8.9 C throughout the entire incubation period.

Nine male and nine female chum salmon were used to test the possible effects of male size and/or age on alevin and fry growth. The fish were spawned so that three sets of a 3 x 3 factorial cross were created. Female size and age were kept constant in each factorial cross, whereas male size and age varied. Three males and three females were spawned at the same time and the egg complement of every female was divided into thirds with each third being fertilized by a different male. In this manner, a total of 27 different crosses was created (Fig. 2).

Each cross or population was kept separate by being incubated in its own Heath tray. Observations were made during the incubation period to determine the number of temperature units required to hatch eggs originating from the different crosses. The wet and dry weights of newly-hatched alevins were also measured. Three groups of three alevins were removed from each cross, blotted dry, and weighed to the nearest .01 g on a Mettler P 120 balance. The groups were then placed in a drying oven and baked at 97 C for 24 hr. After being dried, the alevins were placed into a vacuum dessicator, allowed to cool, and reweighed on the Mettler P 120 balance.

A similar sample of nine fry/population was removed and weighed 102 days after fertilization. Also at this time, three groups of 100 fry from every cross 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 P 1200 balance. Forty to fifty fork lengths (tip of snout to



THE EGG COMPLEMENT OF ♀ A

♀♀ \ ♂♂	1 (3yrs)	2 (4yrs)	3 (4yrs)
A (4yrs)	A x 1 (4 x 3)	A x 2 (4 x 4)	A x 3 (4 x 4)
B (4yrs)	B x 1 (4 x 3)	B x 2 (4 x 4)	B x 3 (4 x 4)
C (4yrs)	C x 1 (4 x 3)	C x 2 (4 x 4)	C x 3 (4 x 4)

A REPRESENTATIVE 3X3 FACTORIAL CROSS

FIG. 2. Three 3x3 factorial crosses were created by spawning three different groups of three males and females at the same time. In making the factorial crosses, the egg complements of every female were split into thirds, with each third being fertilized by a different male. In this fashion, 27 distinct crosses (15 4-year-old ♀ x 4-year old ♂ and 12 4-year-old ♀ x 3-year old ♂) were produced.

fork of tail) were obtained on fry representing each cross by anesthetizing and measuring portions of the previously-weighed fry.

Immediately after sampling, the fry from each population were individually counted and transferred into rearing troughs. The troughs were 30.7 cm x 30.7 cm x 240 cm and divided by wooden-framed nylon-mesh (1/16-inch Delta) screens into three equal rearing areas 30.7 cm x 30.7 cm x 78.5 cm. During the 13-week rearing period, water depth was maintained at 16.5 cm, velocity at 11 liters/min (3 gal/min) and temperature varied between 8.7 C and 8.9 C. Dissolved oxygen concentrations in each trough were determined on a weekly basis by a Hach kit and were moderately low, ranging from 9.8 ppm to 5.4 ppm.

To test for possible location effects within the troughs, the three populations of fry produced from a male were placed into all three possible rearing areas (head, mid, and tail) in three different troughs, whereas the progeny originating from a single female were always reared in the same divided trough. Thus, each trough contained three populations of fry begot by the same female yet fertilized by different males (Fig. 3).

The fry were fed in excess 14 to 16 times/day on an Oregon Moist Pellet diet. During the period they were being reared, each population was sampled once a week. Twenty-five fry were randomly selected from each cross, killed with a heavy dosage of MS-222, and individual lengths (TSFT to the nearest .25 mm) and wet weights (to the nearest .001 g) were then taken. The sacrificed fry were next arbitrarily divided into five lots of five fry each and baked in a drying oven for 48 hr at 97 C. Upon removal from the oven, the fry were placed into a vacuum dessicator, allowed to cool, and weighed to the nearest .001 g on a Mettler P 120 balance.

After 13 weeks of freshwater rearing, the fingerlings were divided

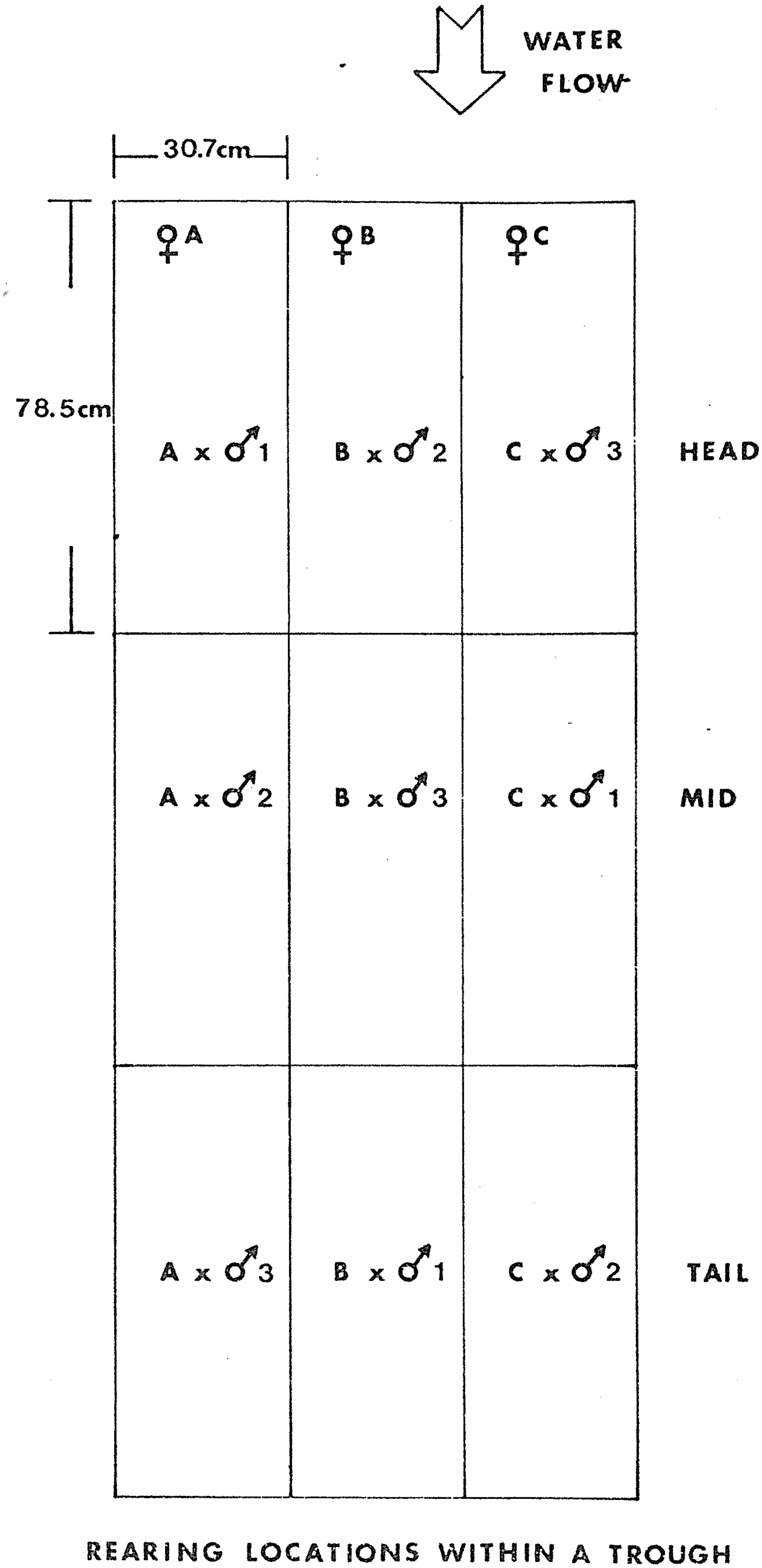


FIG. 3. The rearing locations within a trough for fry begot from a single 3x3 factorial cross.

into two major groups depending upon the age of their male parent. Both groups of progeny were vaccinated against vibriosis and had either the right (4 ♀ x 4 ♂) or left (4 ♀ x 30 ♂) ventral fin removed. For 1 week following their innoculation and fin-clipping, the fish were fed a medicated TM 50 (terramycin) Oregon Moist Pellet diet. They were then transported to Henderson Inlet (Thurston County, Washington State) and are presently being reared in salt water in a 20-ft x 20-ft x 12-ft pen. At this site, the fish will be sampled twice monthly and reared until December 1975.

Possible maternal effects on the developmental rate and size of fry at emergence were also examined. The eggs from three females (one 4-year-old and two 3-year-olds) were fertilized by two similarly-sized 3-year-old males. A sample of eggs from each female was removed at the time of fertilization and allowed to water-harden for 24 hr. After water-hardening, the eggs were run through a series of eight sieves with pore sizes ranging from 8.72 mm to 6.34 mm. The wet and dry weights of the eggs resting on each sieve were then determined.

The remaining fertilized eggs from each female were placed in separate wire egg baskets and hung in rearing troughs. While incubating in the wire baskets, the eggs were kept in total darkness except during periods of routine sampling. Just before hatching, the eggs were removed from their baskets and transferred into Heath trays furnished with Astroturf substrate.

To determine if differences existed in the rate at which the eggs developed, three eggs from each lot were removed daily and preserved in 5% acetic acid. After the eggs hatched, alevins were removed once every

7 days and preserved in 5% Formalin. The yolk and somite material from each alevin were separated and both parts were weighed, dried, and reweighed. At the conclusion of the incubation period, 230 fry from each cross were frozen and will be used to help determine if differences existed in the sex ratios of fry propagated from similarly-or differently-aged parents.

Milt Production

A small experiment was performed to determine if there were any difference in the percentage of water present in milt produced by the same male throughout its freshwater lifetime. Five males were placed in a 1.5-m x 15-m channel section and stripped artificially once every 24 hr. Care was taken to remove any impurities (blood clots, gastro-intestinal residue, etc.) that may have been present in the samples. The volume, wet, and dry weights of the extracted material were then measured.

RESULTS AND DISCUSSION

Basic Behavioral Patterns of Spawning Chum Salmon

In attempting to discover the patterns of mate selection that may exist in chum salmon, it is necessary to examine the social behavior of adults while they are interacting on the spawning grounds. This entails a moderate understanding of species-specific signals which consist of auditory (Neproshin, 1974), olfactory (Newcombe and Hartman, 1973), tactile and visual (Reimers, 1967; Schroder, 1973; Tautz and Groot, 1975) components. Fortunately, it appears that enough of the behavioral repertoire of this species is visually perceivable so that general behavioral patterns can be recognized by simple visual observations.

The basic behavioral patterns of each sex are distinctly different from one another. Females are territorial and may utilize both tactile and chemical clues in finding a suitable spawning site. Once a female has established a territory, she will construct a series of four to six discrete nests and will remain in close proximity to them until she dies. Each nest is formed by a characteristic series of "digging" motions. Typically, the animal rotates onto her left or right side and executes a set of rapid body flexures which causes the caudal fin to be raised and lowered in a series of powerful strokes. As the caudal fin is lifted, a vacuum is created underneath it which sucks up small stones and fine substrate materials that are then carried downstream by water currents. While digging, the pectoral fins are held at a 90-degree angle from the body wall and appear to function as brakes that act to localize a digging effort. While the nest develops, the digging activities of a female are focused into a central depression and eventually, the fish will begin to perform "probing" motions into the nest with her ventral and anal fins (Schroder, 1973; Tautz and Groot, 1975). A probe is initiated when a female inserts her fins into the interstices found between the stones lying at the bottom of her nest and is completed when she lifts herself up and out of the gravel pocket. Tautz and Groot suggest that probing supplies important tactile input to a female regarding both the depth and contour of her nest. When the nest is completed, the female will remain in the probing position with her beak widely agape (crouching)--if accompanied by a male, she will usually release a portion of her eggs while the male in a similar posture simulataneously ejaculates milt.

Immediately after spawning, the female begins to cover her eggs with gravel located laterally and anterior to her nest. The burial process creates a trench in front of the previously-used nest and often becomes the site of the next succeeding one.

In general, females are strongly substrate oriented, with the majority of their attention being directed to nest or mound (the collective burial of all the nests under one large mound of gravel) construction. Prolonged aggressive interactions between females rarely transpire , with the preponderance of intrasex aggression being directed at territorial females less than 2 m away (Schroder, 1973).

Males do not establish permanent territories but tend to be mobile, moving from one territorial female to another. Aggression among males is common, and prolonged ritualistic challenges and battles may occur between similarly-sized rivals. Such battles usually occur directly over the contested female's nest site and often prevent other males from courting and spawning with her. Physical size, strength, stamina, and persistence appear to be important attributes which may help determine how successful a male is in courting and spawning with females.

Males own a repertoire of characteristic courting movements that appear to be closely attuned to the digging and probing activities of the female (see Tautz and Groot for an account of the frequencies of courtship and other related reproductive behaviors in chum salmon). After spawning, a male will remain by a female for approximately 20 min or less (often drifting away and returning at infrequent intervals) before he abandons her, possibly locating another whose nest is nearer to being completed and hence, closer to spawning.

Both sexes tend to be opportunistic and promiscuous and thus, it is possible for a female's eggs to be fertilized by four or more different males. If there are more males than females on the spawning grounds or if the population of spawners is numerous enough to limit the numbers of females that can find and hold territories (producing a situation where males will outnumber females with territories), then more than one male quite often spawns with a female at the completion of her nests. Consequently, so-called satellite males can increase the number of sexual partners that may fertilize portions of a female's egg complement.

Dominant, or alpha, males can be easily distinguished from satellite males by their color patterns, courting movements, and close downstream proximity to a female. When observations were made to determine whether chum salmon paired in a predictable pattern, only the size of the alpha male (often only one male was present) was used to calculate the size ratio that existed between a courting pair. Furthermore, it sometimes happens that a male may fertilize more than one clutch of eggs a female deposits. When such cases were observed, the size ratio of the pair was used only once. It was felt that since size preference was being examined, the inclusion of multiple spawnings by the same pairs might mask any emerging tendencies.

The results of these observations are shown in Figs. 4 to 8. Each figure indicates what the expected (random) and observed frequencies of pairings were between fish of various size ratios (male body wt:female body wt). To test whether these frequencies were statistically similar, a Goodness-of-Fit Test (G statistic, Sokal and Rohlf, 1969) was used (Table 1). This test indicated that when the sex ratio was at parity or

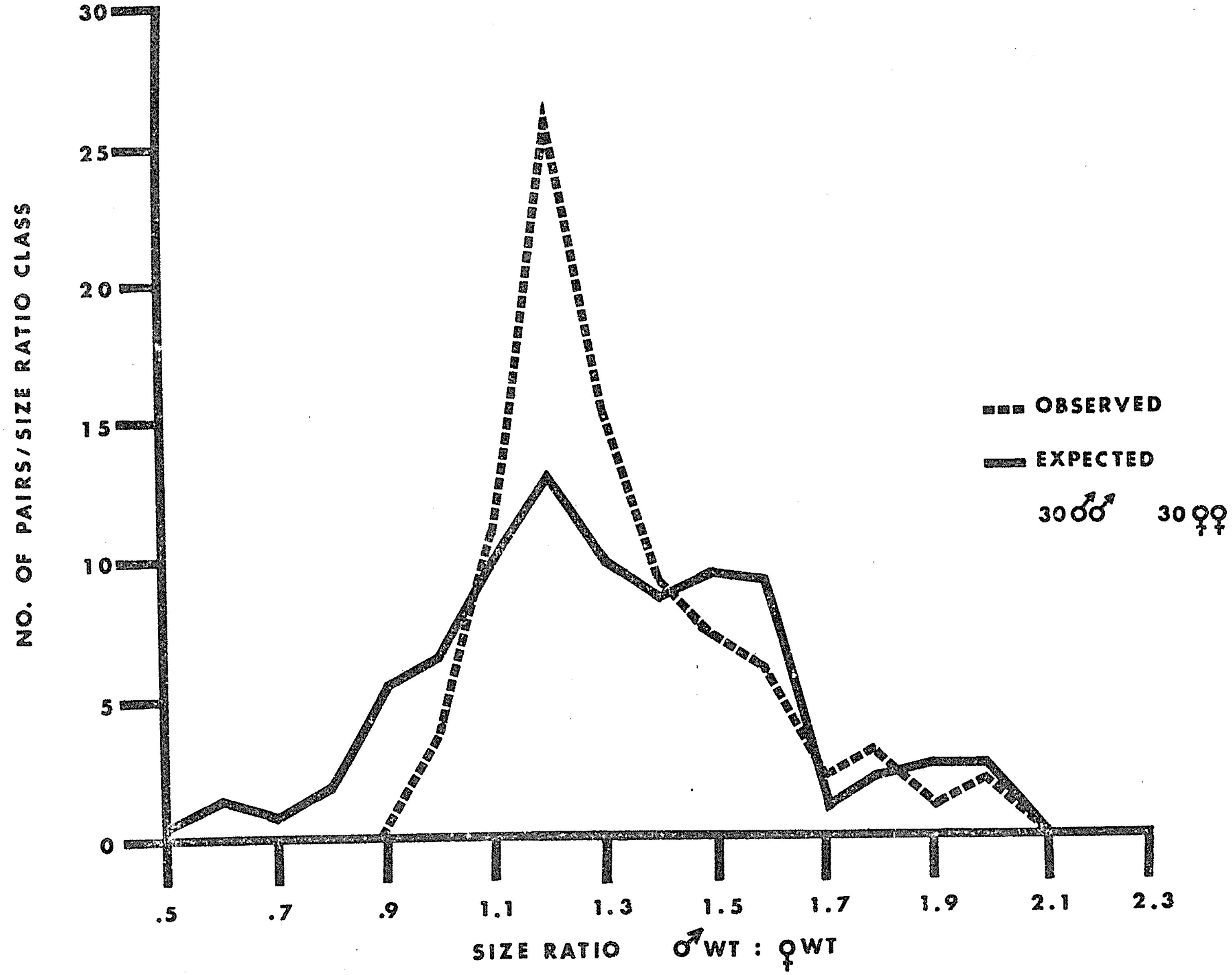


FIG. 4. The expected (random) and observed frequencies of pairings between mating chum salmon of various size ratios (♂ body weight: ♀ body weight) at a sex ratio of 1:1 and a spawner density of 1.55 m^2/♀.

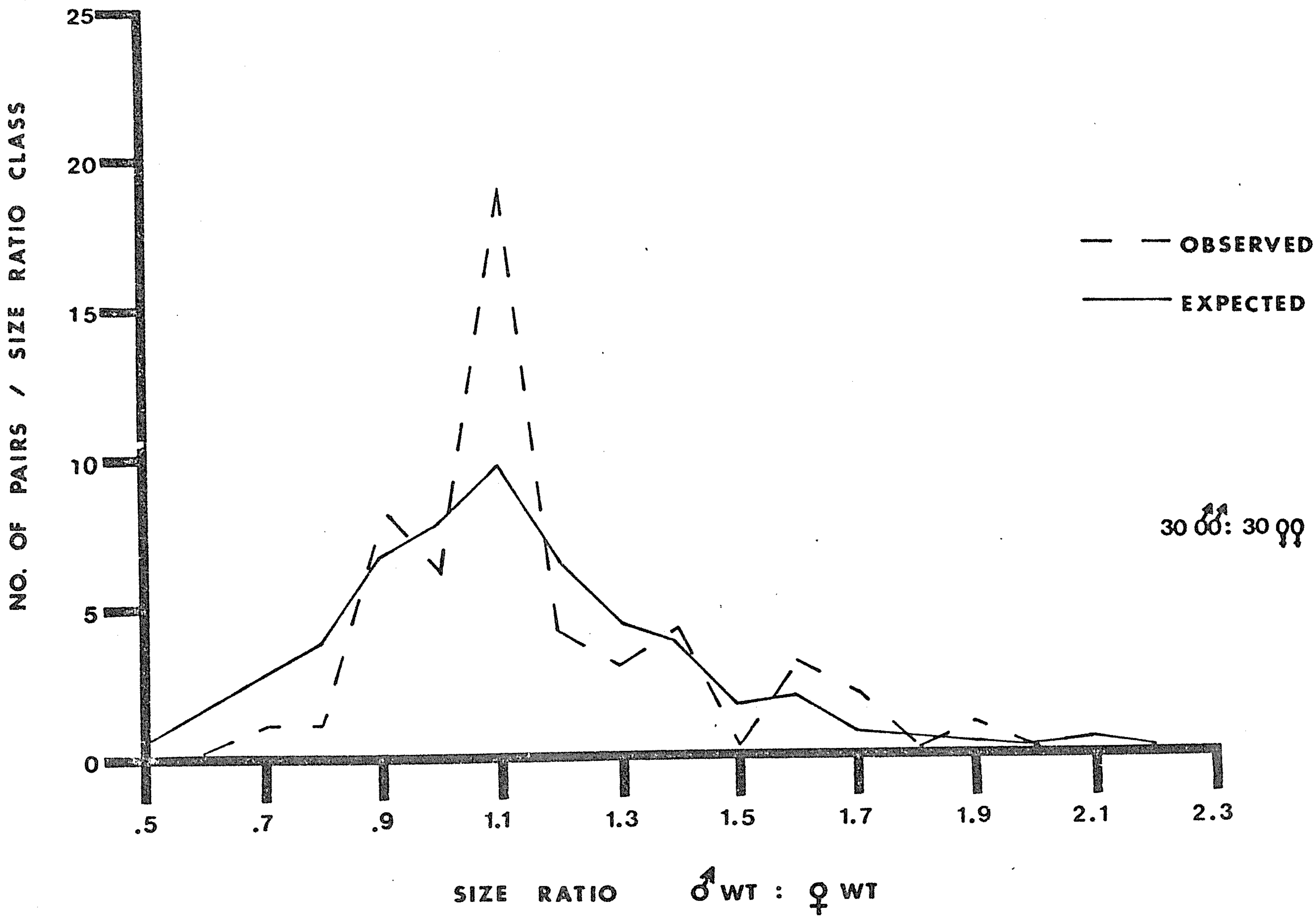


FIG. 5. The expected (random) and observed frequencies of pairings between mating chum salmon of various size ratios (♂ body wt:♀ body wt) at a sex ratio of 1 ♂:1 ♀ and a spawner density of 1.55 m^2/♀.

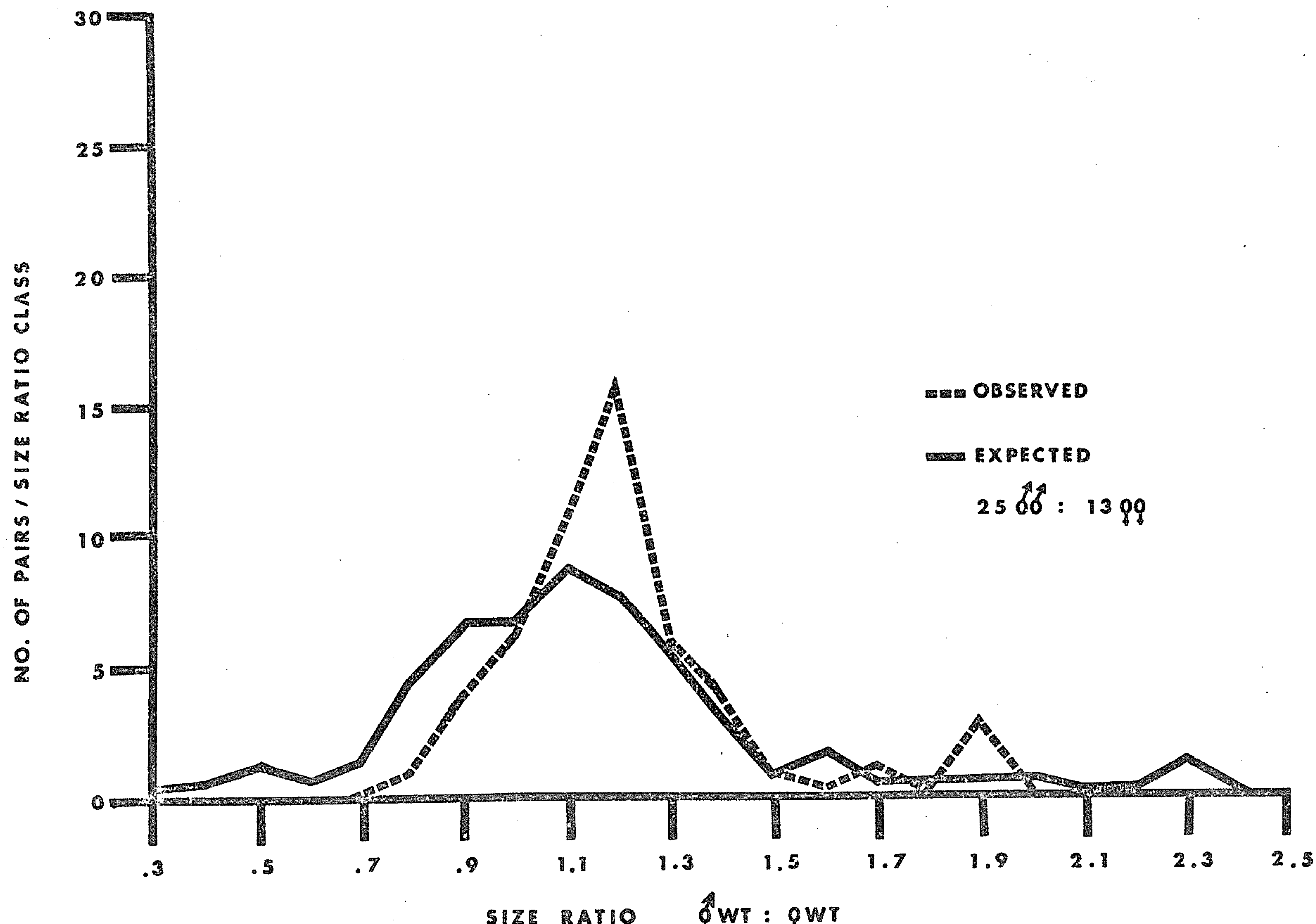


FIG. 6. The expected (random) and observed frequencies of pairings between mating chum salmon of various size ratios (♂ body wt:♀ body wt) at a sex ratio of 2 ♂♂:1 ♀ and a spawner density of 3.58 m^2/♀

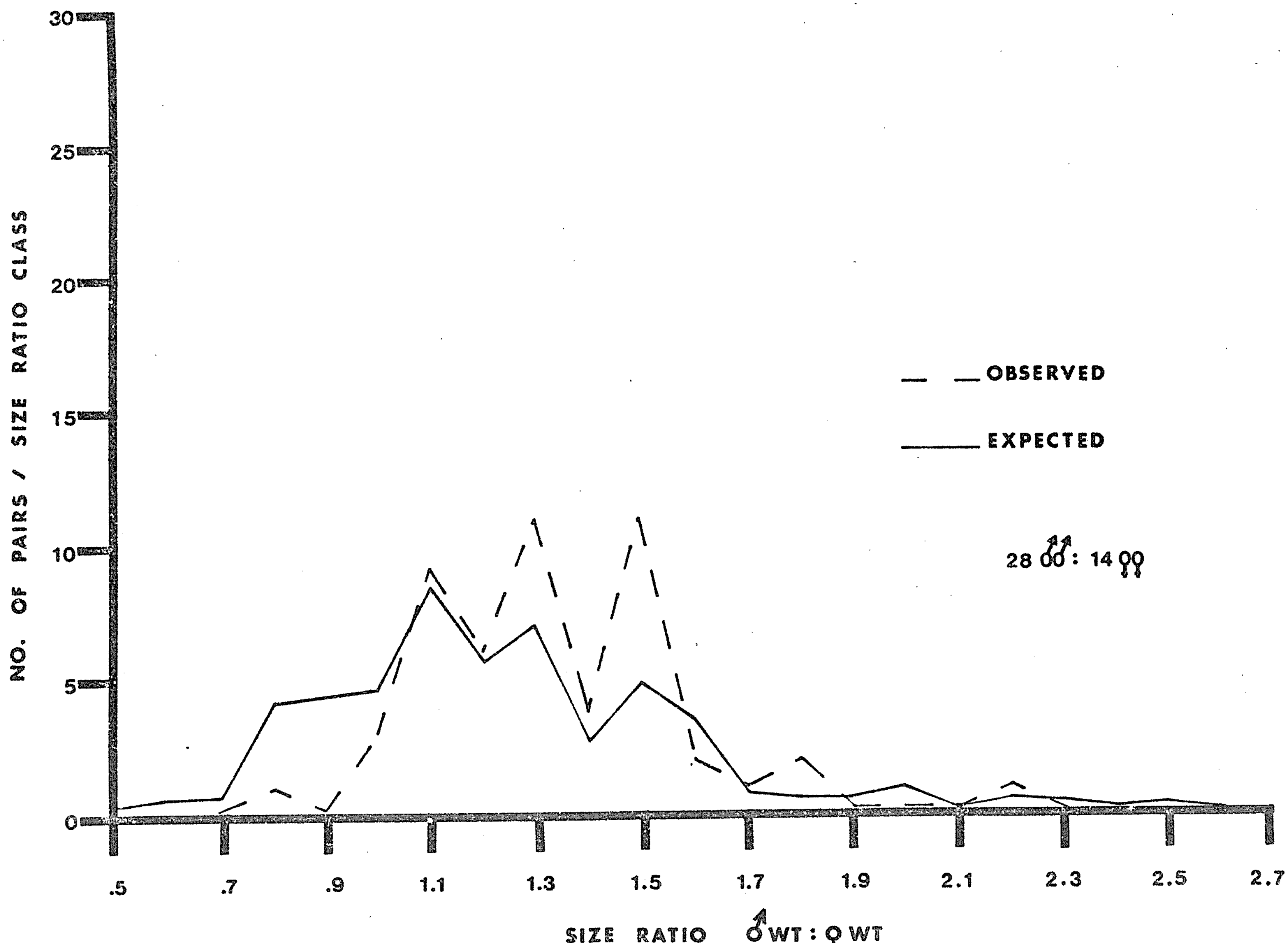


FIG. 7. The expected (random) and observed frequencies of pairings between mating chum salmon of various size ratios (♂ body wt:♀ body wt) at a sex ratio of 2 ♂♂:1 ♀ and a spawner density of $3.32m^2$/♀.

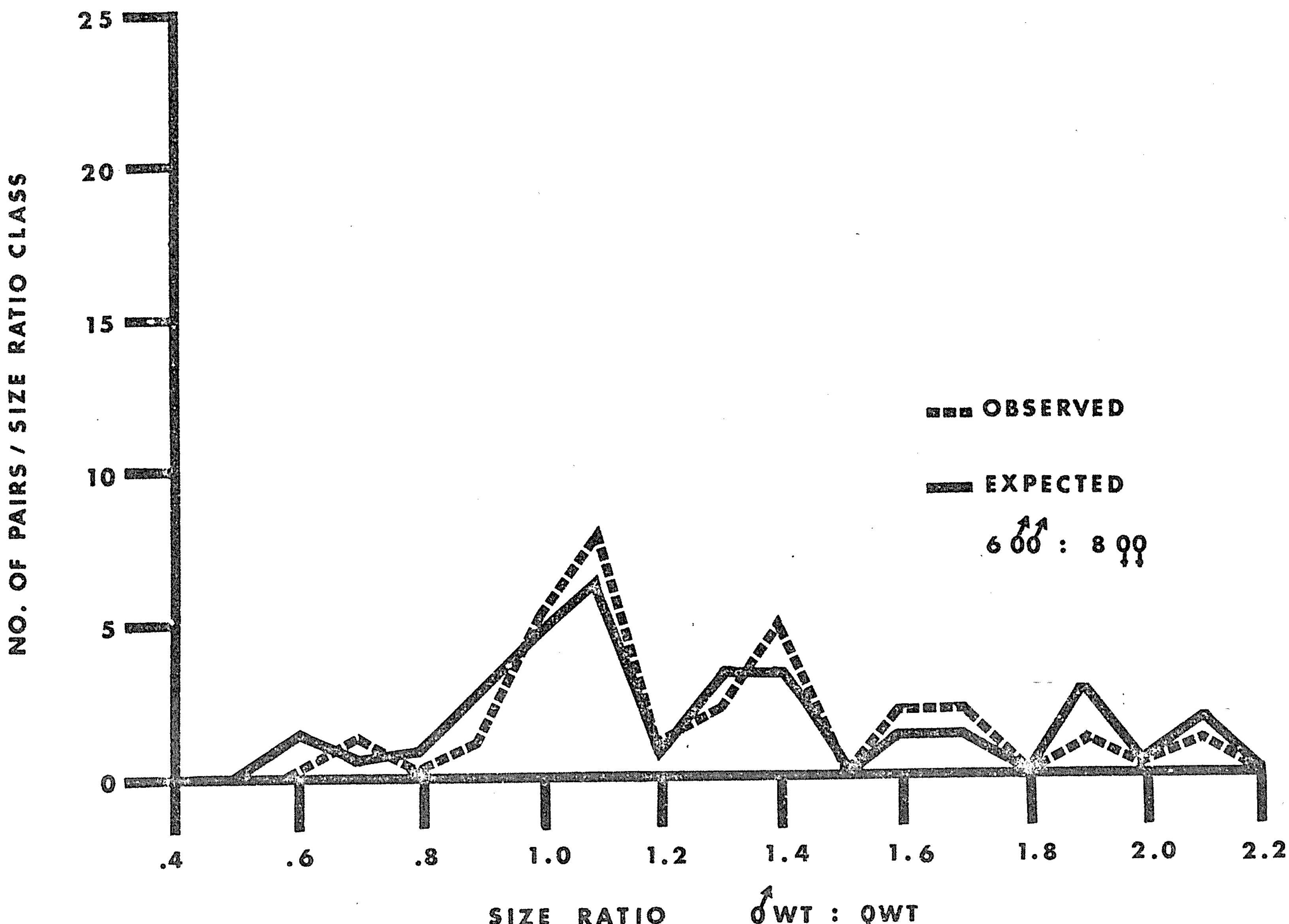


FIG. 8. The expected (random) and observed frequencies of pairings between mating chum salmon of various size ratios (♂ body wt:♀ body wt) at a sex ratio of .75 ♂:1 ♀ and a spawner density of 5.81 m^2/♀.

Table 1. The results of Goodness-of-Fit Tests used to evaluate whether observed outcomes of mate selection in chum salmon were similar to those which would occur if mates were chosen at random

Density of spawners m²/♀	Sex ratio ♂:♀	Number of ♀	G statistic value and significance
1.55	1:1	30	$44.3 > X^2_{.05(15)} = 24.9$
1.55	1:1	30	$32.2 > X^2_{.05(15)} = 24.9$
3.58	2:1	13	$48.5 > X^2_{.05(20)} = 31.4$
3.32	2:1	14	$43.4 > X^2_{.05(21)} = 32.7$
5.81	.75:1	8	$18.6 < X^2_{.05(15)} = 24.9$

when there were more males than females, pairing did not occur randomly. Visual inspection of the figures suggests that chum salmon preferentially pair with individuals of approximately the same size. In most cases, if a male was smaller than a female, he was rarely able to exclusively court or spawn with her. Conversely, males that were larger than their prospective mates were often successful. Table 2 depicts the size ratios that existed between males and females originating from various brood years. By comparing these size ratios to those which existed between the observed pairs, it can be seen that mate selection in this species is often assortative with respect to both size and age.

Figs. 6 and 7 illustrate that subtle changes may also occur in the size ratios of pairs that form when spawner density is moderate (< 4 m^2/female) and there are twice as many males as females. Under these circumstances, competition among male rivals is intense and consequently, the size and strength of a male are given additional importance. However, when spawner density is low (> 4 m^2/female) and the number of gravid females holding territories exceeds the number of males present, then mate selection tends to lose its assortative properties and mating becomes random (Fig. 8).

<u>Color Patterns in Spawning Chum Salmon</u>

Other results that originated from the mate-selection observations dealt with the dynamic characteristics of the nuptial color patterns found on both sexes. Chum salmon that enter Big Beef Creek to spawn are sexually dimorphic and have distinctive color patterns consisting of greens, purples, yellows, blacks, and whites. The females are fusiform in shape and usually have a horizontal purple and black band that

Table 2. The size ratios* existing between male and female chum salmon originating from similar and different age classes (subpopulations) at the time of their migration into Big Beef Creek.

Age of ♂	Age of ♀	$\bar{x}$ size ratio (♂ wt : ♀ wt)
4	4	1.199
4	3	1.651
3	4	.805
3	3	1.108

* Male body weight;female body weight
Based upon 166 4-year-old females
49 3-year-old females
29 3-year-old males
30 4-year-old males

longitudinally bisects the lateral body wall. The rest of the body is light to dark green except for the belly and the tips of the anal, ventral, and often dorsal fins, which are white. Males are more laterally compressed, possess distorted jaws armed with canine-like teeth, and commonly have vertical streaks of purple and black that overlie a mottled green background.

A subtle change was observed in the color pattern of females as they developed individual nests. As the construction of a nest progressed, the color of the belly gradually became darker, often changing into a dark purple at the time of egg deposition. The significance of this color change is not known, but it may serve to advertise the reproductive status of a female.

Unlike females, males are capable of quickly altering their color patterns between those which are typically male or female in appearance. Kees Groot (personal communication), in an ingenious experiment, demonstrated that a male's social position (dominance) relative to other male rivals is reflected by his color pattern. Adult chum salmon were placed into an aquarium and allowed to form pairs complete with satellite males. At this time, a broom handle was used to strike repeatedly at the sides of an alpha male. Invariably, the attacked male quickly lost his male color pattern and resembled a female. Once the attack was completed, the alpha male would nip at male subordinates and eventually reacquire the typical male color pattern. Table 3 enumerates the occurrence of the two-color morphs present on alpha and satellite males found in three sections of the Big Beef Creek spawning channel. This table indicates that subordinate males commonly resemble females.

Table 3. The occurrence of two-color morphs on chum salmon males of various social status

Density of spawners $m^2/♀$	Sex ratio ♂ : ♀	Color morphs present on courting males				Color morphs present on satellite males			
		♂ pattern observ.		♀ pattern observ.		♂ pattern observ.		♀ pattern observ.	
		No.	%	No.	%	No.	%	No.	%
3.32	2:1	79	92	7	8	0	0	21	100
3.58	2:1	75	93	6	7	1	2	47	98
1.55	1:1	64	97	2	3	0	0	19	100

Fig. 9 shows the percentage of time that males of different size classes spent in each color morph under various sex ratios and spawner densities. These data substantiate the idea that large males are often dominant over smaller ones and consequently may have greater access to females under certain sex ratio and spawner density regimes.

The occurrence of a "submissive color pattern" should not be surprising since ritualistic fighting does occur in this species. Certainly, this type of communication tends to prevent both serious depletion of energy stores and injuries. Mechanically ritualized fighting and less elaborate aggression often determines which males will be allowed to spawn with available females. Size is not the sole determining factor in such contests; the physical condition and/or persistence of a male are also important factors. Fig. 10 suggests that as a male ages in freshwater and becomes more weakened, the percentage of water present in his milt gradually increases. It is speculated here that higher water content in male ejaculate may influence the fertility of the animal. Hence, ritualized battles and other forms of aggression may select against weakened and possibly less fertile males of any size class.

Viewing Chamber Observations

Most of our discussion has tended to emphasize the role of male mobility, size, and aggression in the processes involved in pair formation. Groot (personal communication) has suggested that three conflicting drives (fear, aggression, and sex) exist in spawning salmon and that a compromise has to be reached among these drives before spawning can occur. Under

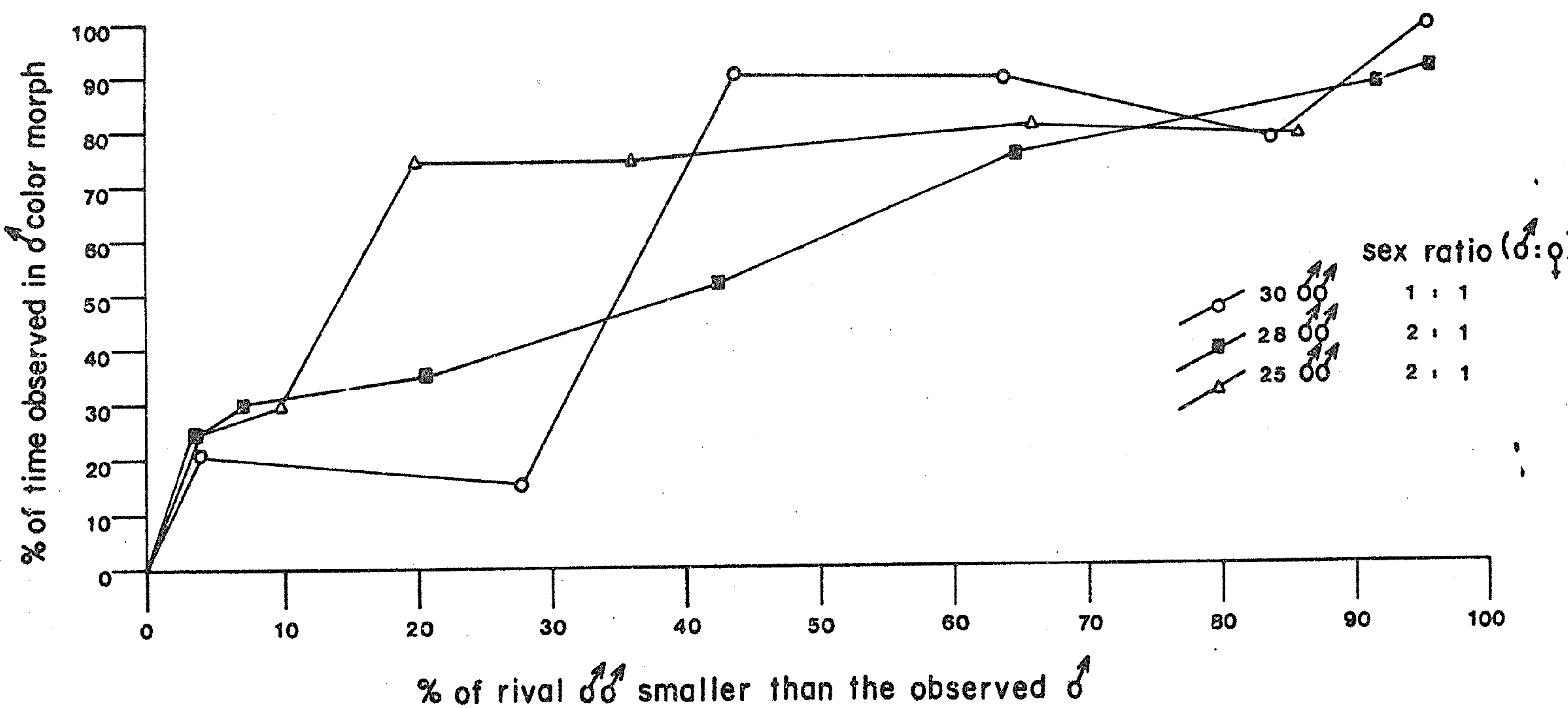


FIG. 9. The percentage of time that chum salmon males of different sizes spent in the male color morph under various sex ratios and spawner densities.

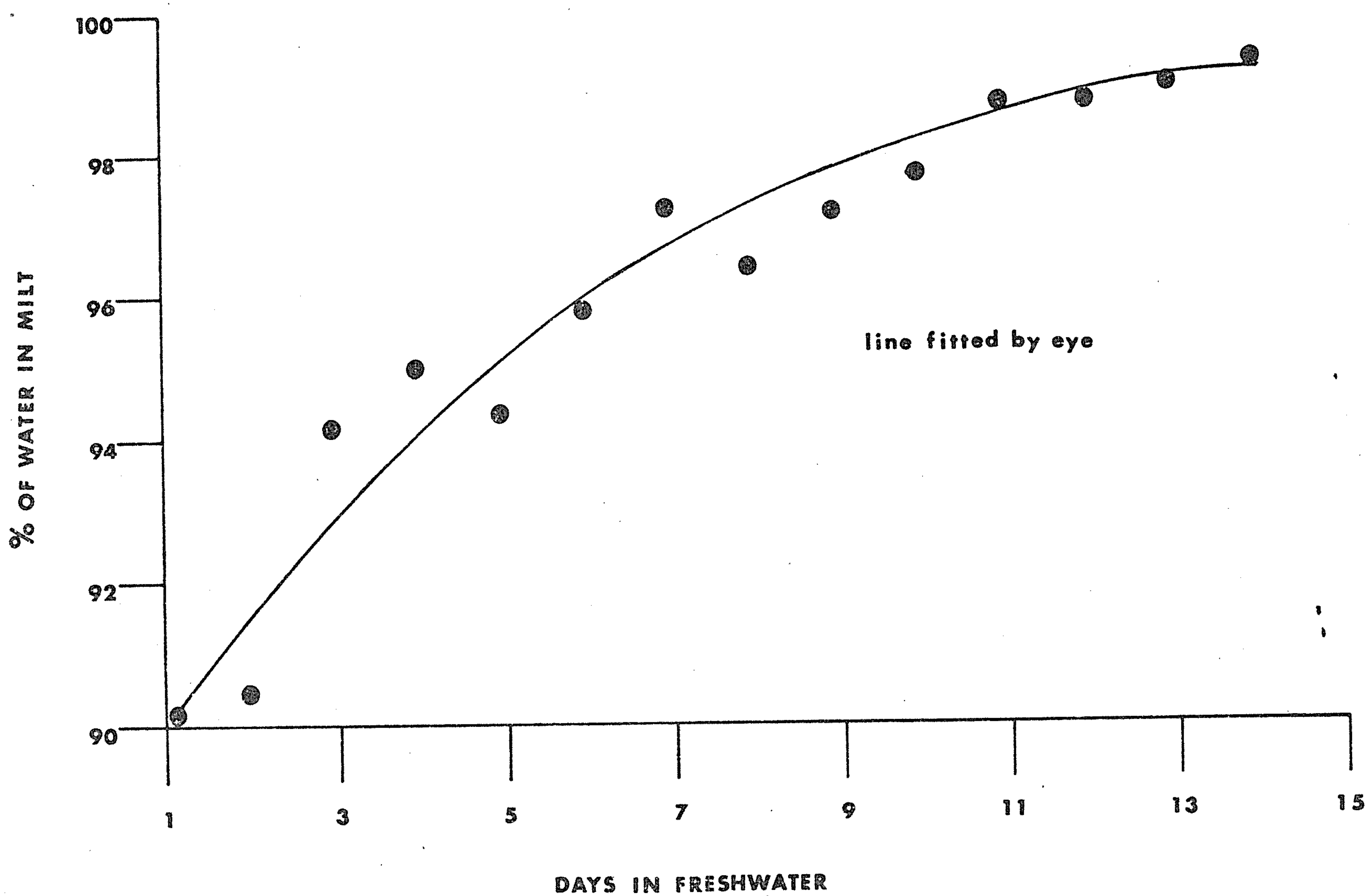


FIG. 10. The relationship existing between the spawning ground residency of a male chum salmon and the percentage of water present in his milt.

this hypothesis, it might be expected that pairs consisting of similarly-sized fish would reach a compromise among their drives sooner than those comprised of more divergent individuals. This speculation supposes that courting fish may be more prone to perform comfort movements[1], attack, or flee from one another if they are very dissimilar in size.

Hence, the ability of spawners to compromise their internal drives while courting could influence the occurrence of pairs representing various size ratio classes. For example, if a male were smaller than the female he was courting and this led to the predicted increase of comfort movements and aggression within the pair, then the rate at which the female developed her nest could be considerably slowed. This would extend the amount of time the male would be vulnerable to challenges from other potential suitors. Additionally, any delay in nest preparation may also increase the probability that the original male may flee or wander away from the female in an attempt to locate a more suitable partner.

To test these ideas and to document the incidences of comfort movements in pairs of fish representing various size ratio classes, 11 pairs of fish were individually placed in a viewing chamber and filmed with videotape. Preliminary analysis of the videotapes was concerned with the time it took for nest construction, spawning, and number of digs/nest. It was difficult to differentiate when a female had finished burying one nest and started upon another as material excavated from a

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[1]See Baerends and Baerends Von Roon (1950) for a formal definition of comfort movements. In this species, such movements appear to include:

a) Yawning - the prolonged opening of the beak
b) Spitting - a quick snapping motion of the beak
c) Weaving - swimming in a circular or weaving fashion over the nest site

single dig may simultaneously accomplish both activities. To allow comparisons among the pairs representing various size ratio classes, the moment that nest construction began for the first, second, and third nests was arbitrarily standardized. A female's initial nest was thought to have started at the time she executed her first dig. Similarly, the second and third nests were considered to have begun during the first dig that occurred immediately after spawning. A more detailed analysis of the behavioral interactions among members of courting pairs (in particular, the frequencies of various comfort movements) and between the female and the substrate is underway, but will not be discussed in this report.

Table 4 and Fig. 11 suggest that both the physiological condition of the female and the size ratio of the pair play important roles in determining how rapidly a female develops her nests. One may wonder if the time differences illustrated in the data are of any biological consequence. It should be remembered that while the pairs were being filmed they were not interrupted by conspecifics and hence, the data theoretically represent the minimum amount of time a female would spend in developing a nest. Clearly, the amount of time and energy allocated to both males and females during their reproductive cycle is limited and hence, any factor that delays them from spawing may influence their ultimate reproductive success.

If the above premise is true, why is there any difference between the time it takes females with variously-sized male partners to develop their nests? It was this general question that prompted the investigations into the egg characteristics of differently-aged females and the growth

Table 4. Videotape analysis of the time and digging motions* required to complete single nests by female chum salmon with variously-sized male partners

Size ratio of spawning pairs ♂ body wt:♀ body wt	First nest		Second nest		Third nest	
	Time in min	Number of digs	Time in min	Number of digs	Time in min	Number of digs
.5:1	106	142	159	271	-	-
.42:1	874	294	214	389	-	-
.69:1	94	86	200	295	-	-
.46:1	232 $\bar{x}$ 326	126	203 $\bar{x}$ 194	281	-	-
1.1:1	127	149	133	246	-	-
1.2:1	210	220	-	-	-	-
1.1:1	74 $\bar{x}$ 137	-	123 $\bar{x}$ 128	218	148	256
2.2:1	74	94	115	245	118	279
2.0:1	128	174	121	238	157	273
1.7:1	136 $\bar{x}$ 113	163	136 $\bar{x}$ 124	228	-	-
3.5:1	93	73	184	237	-	-

* Includes covering digs on second and third nests

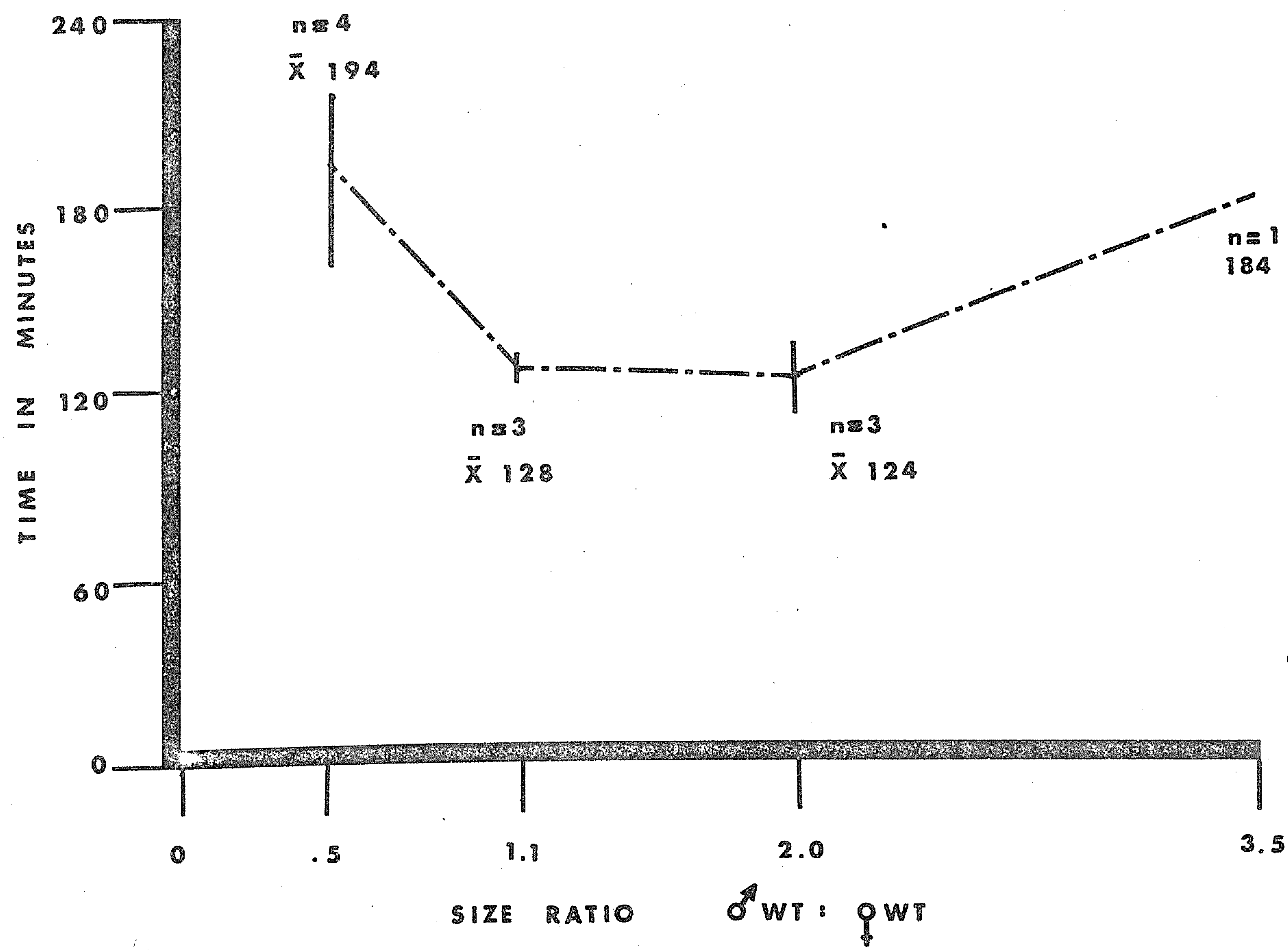

FIG. 11. The time required for female chum salmon with variously-sized male partners to complete their second nest (includes covering the first nest through egg deposition in the second nest).

patterns of progeny produced from selected artificial crosses. If it could be demonstrated that some advantage would be bestowed upon progeny produced from certain types of matings, then it would make biological sense for both sexes to have evolved the ability to discriminate between potential mates of various sizes and ages.

The Egg Characteristics of 3- and 4-year-old Chum Salmon Originating from the Middle Run of Big Beef Creek

An array of geophysical properties are probably unique to each stream or lake area that salmon utilize as spawning areas. If any of these environmental factors are constant over a period of many generations, then specific adaptations are likely to evolve that circumvent or exploit these predictable environmental qualities. Consequently, one would expect that egg number, size, pigmentation, potential nutritive content and other attributes are adapted to traditionally existing conditions. Because streams are often dynamic and may alter their potential incubation environments quickly, it is probable that eggs originating from salmon spawning in unstable systems (such as many streams) may be able to withstand an unpredictable environment better than those deposited in a traditionally less dynamic one. One may speculate further and suggest that there should be less variability and more unique specific adaptations in the physical properties of eggs originating from stable incubation environments.

In either circumstance, it follows that there should be an optimum range of egg sizes, nutritive content, etc. for each ancestral spawning ground. The portions of Big Beef Creek that have been traditionally used by the middle run of chum salmon have proven to be unstable (Cederholm, 1972) and therefore present an unpredictable challenge (of varying intensity) to incubating eggs. The morphometric properties of both the females and eggs originating from the middle run are presented in Tables 5 and 6. The tables are designed to allow comparisons between 3- and 4-year-old females which represent the dominant age classes returning to this stream. Not unexpectedly, 4-year-old females are larger and produce bigger eggs than 3-year-olds.

Linear regression analyses were used to test whether correlations existed between a female's age, weight, length, and condition factor and the diameter, weight, and condition factor of her eggs. These tests indicated that there was little linear correlation between the physical characteristics of 4-year-old females and their eggs. Yet, moderately strong correlations did exist between these characteristics (except female condition vs. egg condition) in 3-year-old fish.

Because the eggs produced from variously-sized females originating from one population are subjected to similar selection pressures, it should not be too surprising that there are moderate or low correlations between a female's physical parameters and the size of her eggs. Since each egg costs a certain expenditure of energy to produce, it may be expected that rapidly-growing and/or longer-lived individuals can afford to produce more eggs. Koski (1975) and Schroder (1973) have both presented data indicating that fecundity does increase with female size in chum salmon originating from Big Beef Creek and have cited other

Table 5. A comparison between the lengths, weights, condition factors*, and egg parameters of 3- and 4-year-old females migrating into Big Beef Creek during November and December 1974

Age	Length		Weight		Condition factor		Egg diameter		Wet egg weight		Dry egg weight		Condition factor**	
	$\bar{x}$ value	SD	$\bar{x}$ value	SD	$\bar{x}$ value	SD	$\bar{x}$ value	SD	$\bar{x}$ value	SD	$\bar{x}$ value	SD	$\bar{x}$ value	SD
4	735 mm	29 mm	4.7 k	.6 k	1.17	.07	7.16 mm	.24 mm	.27 gr	.025 gr	.105 gr	.010 gr	.735	.046
3	664 mm	37 mm	3.4 k	.6 k	1.15	.12	6.72 mm	.22 mm	.23 gr	.021 gr	.088 gr	.088 gr	.742	.030

* Condition factor = (body weight/fork length^3) x 10^5

**Egg condition factor = (weight egg weight/egg diameter^3) x 10^3

SD = Standard deviation

Table 6. Conditional* linear regression analyses between the morphometric characteristics of 3- and 4-year-old chum salmon females and their eggs.

Age	X variable	Y variable	r	r^2	B value	t test B = 0	Significance > .05
4	wet egg wt.	Body weight	.387	.150	9574	5.104	Yes
3	wet egg wt.	Body weight	.693	.481	20421	6.461	Yes
4	dry egg wt.	Body weight	.432	.187	26815	5.828	Yes
3	dry egg wt.	Body weight	.723	.522	51892	7.016	Yes
4	wet egg wt.	Fork length	.308	.095	357	3.943	Yes
3	wet egg wt.	Fork length	.622	.387	1114	5.335	Yes
4	dry egg wt	Fork length	.367	.134	1063	4.793	Yes
3	dry egg wt	Fork length	.657	.432	2868	5.848	Yes
4	Egg diam	Body weight	.335	.112	864	4.325	Yes
3	Egg diam	Body weight	.724	.524	2003	7.045	Yes
4	Egg diam	Fork length	.276	.076	33	3.487	Yes
3	Egg diam	Fork length	.638	.408	107	5.564	Yes
4	Egg Condition**	Condition Factor	.054	.003	.079	.663	Non-linear relationship
3	Egg Condition	Condition Factor	.091	.008	.376	-.613	Non-linear relationship

*Linear regression analysis assumes that the independent variable X is fixed and measured without error. In the above analyses the independent variables were measured with error and hence the standard (Model I) tests for significance may not be applicable to this data unless we assume it is a typical Berkson case. The Berkson case assumes that the independent variables are measured with error but that the X values and the error terms associated with them are not correlated thus allowing one to use the so-called Model I regression methods for tests of significance (Sokal and Rohlf, 1969). Because these assumptions were made, the regression analyses have been labeled "conditional" to differentiate them from typical Model I or Model II regression analyses (McCaughran, personal communication).

**Egg Condition Factor = (Wet egg wt/Egg diameter^3) X 10^3.

investigators who observed the same relationship in this species in Asia and North America.

Eggs originating from 4-year-old females appear to have a greater nutritive value than those produced by younger fish and thus, might be able to withstand a more rigorous incubation environment. Koski (1975) demonstrated that fry produced from 4-year-old females weighed more upon their emergence than those produced from 3-year-old fish even though the diameter of the eggs was the same. This result may have been caused by a difference in the nutrients within the eggs and/or the presence of a different relationship between egg weight and diameter in 3- and 4-year-old fish. If it could be shown that egg diameters and dry weights were linearly related, then it would be possible to test with an analysis of covariance whether there were differences in the weights of eggs with similar diameters produced from differently-aged females. Linear regression analyses were performed and strong linearity was shown to exist between these two variables in the eggs begot by both year-classes (Table 7). The analysis of covariance indicated that the slopes but not the levels of the two regression lines were similar at the .05 level (Table 8). This implies, as Fig. 12 illustrates, that eggs from 4-year-old females are lighter at a given diameter than those originating from 3-year-olds.

To determine if a relationship existed between egg and fry weight, a linear regression analysis was completed that compared the dry weights of eggs and fry produced from nine 4-year-old females. The results of this analysis (Table 9) and data presented in Fig. 13, which shows how the dry weights of both somite and yolk materials in three batches of

Table 7. Conditional linear regression analyses between the diameter and dry weights of eggs begot by both 3- and 4-year old chum salmon originating from the middle run of Big Beef Creek

Age	Relationship		Regression formula	r	r^2	F ratio		t test B = 0	
	X variable	Y variable				Value	Significance .001	Value	Significance .001
3	dry egg wt	egg diam	$\hat{y}$=4.733+22.619(x)	.871	.759	141.9	yes	11.912	yes
4	dry egg wt	egg diam	$\hat{y}$=5.288+17.875(x)	.743	.552	182.7	yes	13.516	yes

Table 8. An analysis of covariance on the linear relationships observed between egg diameter and dry weight in 3- and 4-year old chum salmon

Age group females	df	Σy^2	Σxy	Σx^2	df	Residuals s.s	Residuals m.s.
4 years	149	8.7986	.2719	.0152	148	3.939	
3 years	46	2.2156	.0744	.0033	45	.534	
				totals	193	4.473	.02318
		Difference for testing slopes			1	.061	.06054
	195	11.0142	.3463	.0185	194	4.534	.02337
		Difference for testing levels			1	.225	.22516
	196	17.8392	.6121	.0286	195	4.758	

For differences in slope $F = 2.6120 < F_{.05}\ (1,193) = 3.92$ therefore fail to reject the null hypothesis at the .05 level

For differences in level $F = 9.6357 > F_{.05}\ (1,194) = 3.92$ therefore reject the null hypothesis at the .05 level

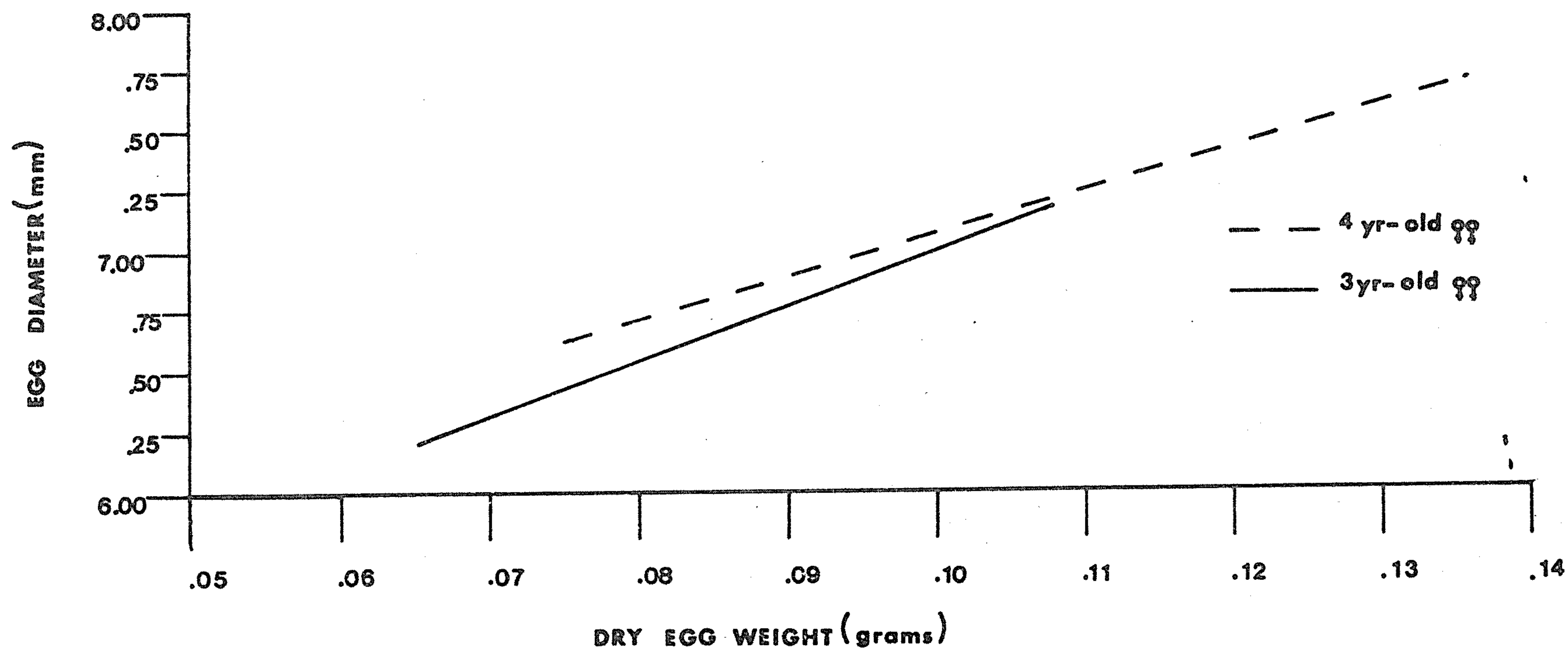

FIG. 12. The linear relationships observed between egg diameter and dry weight in 3- and 4-year-old chum salmon originating from the middle run of Big Beef Creek.

Table 9. A conditional linear regression analysis between the dry egg weights of nine 4-year old females and dry weights of their 102-day-old alevins

Relationship		Regression formula	r	F ratio		t test B = 0	
x variable	y variable			Value	Significance $> .001$	Value	Significance $> .001$
Dry egg wt	dry alevin wt	$\hat{y} = .0305 + .3938\ (x)$	.724	27.47	yes	5.241	yes

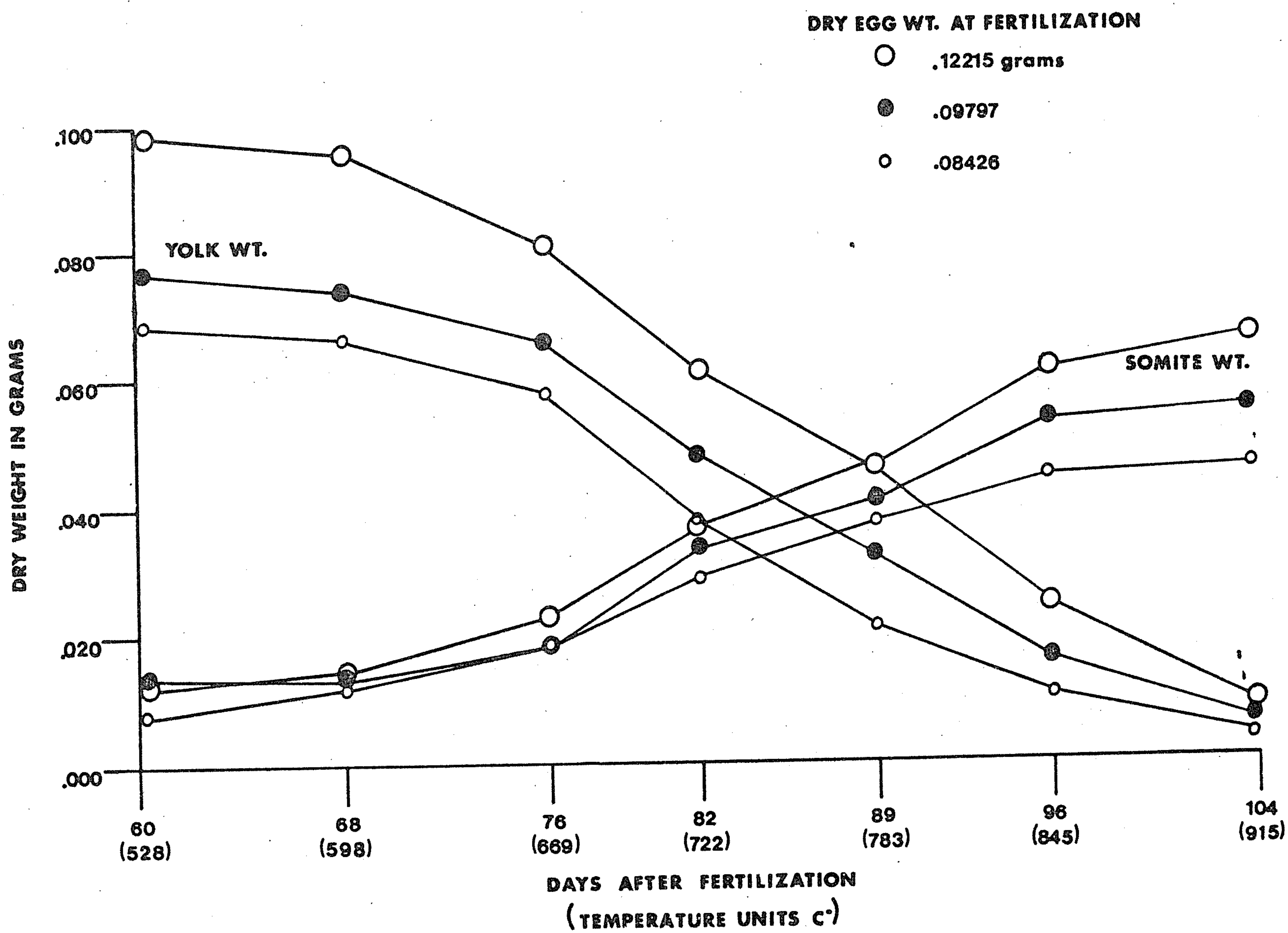

FIG. 13. Temporal changes in the dry weights of both yolk and somite materials in alevins produced from three batches of differently-sized eggs.

differently-sized eggs changed throughout their incubation periods, corroborate earlier findings by Koski (1975) that suggested a strong positive linear relationship between egg weight and fry size at emergence.

Parental influences on embryo growth rates and efficiency of yolk material utilization were also examined. It was found that egg weight did not influence the temperature unit requirements of eggs originating from 4-year-old females (analysis of variance $F = 2.88 < F_{.05\ (5,6)} = 4.39$). However, it was discovered that eggs produced by 4-year-old females hatched sooner when they were fertilized by 3-year-old males than if by 4-year-old fish (analysis of variance $F = 4.8405 > F_{.05\ (1,\ 25)} + 4.24$). Withler and Morley (1970) examined the hatching times of interspecific hybrids made among sockeye, chum, and pink salmon (O. gorbuscha) and concluded that the female parent determined the embryo size at hatching that the male parent controlled the rapidity at which the embryo reached this point, and therefore influenced the time at which the egg would hatch. It is speculated here that the inequalities observed in hatching times due to male age may reflect intrinsic differences in the metabolic characteristics of 4- and 3-year-old males.

Conversely, how efficient the embryo was in utilizing the energy resources of its egg was not influenced by the age of its male parent (analysis of variance $F = .01420528 < F_{.05\ (1,\ 16)} = 4.49$) but appeared to be negatively correlated with dry egg weight, implying that embryos produced from smaller eggs were somewhat more efficient than those originating from larger ones (data gathered on nine different groups of eggs originating from 4-year-old females, Table 10).

Table 10. A conditional linear regression analysis on the relationship between dry egg weight and embryo efficiency in the utilization of yolk materials

Relationship		Regression formula	r	F ratio		t test B = 0	
x variable	y variable			Value	Significance $> .001$	Value	Significance $> .001$
dry egg wt	% of dry egg wt converted to dry alevin wt	y = 98.25 - 282.04 (x)	-.595	13.928	yes	3.732	yes

Fish Culture Results

Data gathered on the growth characteristics (weekly changes in dry weight) of reared fry produced from artificial crosses were analyzed by multiple regression analysis and analysis of covariance which incorporated dummy variables. First, the influence of seven variables (time reared, egg weight, age of male parent, rearing location within a trough, kg of fry/m^3, g of fry/liter/min, and absolute flow rate of water through a trough) on the dry weights of fry originating from each of the 27 experimental populations was determined by using multiple regression analysis. These variables were found to account for 96% of the observed variance in the dry weight values of the examined fry.

To determine if any of the variables could be eliminated from further analysis, it was necessary to divide the explained sum of squares into components attributable to each independent variable. This was done by using the standard regression method where each variable is treated as if it had been added to the regression equation in a separate step after all the other variables had been included (Nie, et al, 1975). The results of this stepwise regression are shown in Table 11 which illustrates the calculated F ratios used to test the significance of the regression coefficients of each variable used in the equation. This analysis indicated that the absolute flow rates of water within the rearing troughs had little effect on dry weight values and consequently, this variable was excluded from further analysis.

Second, by using analysis of covariance with dummy variables, it is possible to determine whether a regression model with several lines will reduce the variability of Y to a greater extent than one with only

Table 11. Results of a stepwise regression analysis on chum salmon fry rearing data

Multiple Regression

Dependent variable: Log 10 transformation of the dry weights of sampled fry

Step	Variable	Simple r	F to enter or remove	Significance
1	Time reared	.972	35163.82	.001
2	Dry egg weight	.099	397.22	.001
3	Fry wt/liter/min	.573	170.32	.001
4	Male age	-.023	38.49	.001
5	Fry wt/m^3	.804	9.82	.002
6	Rearing location	-.024	4.99	.026
7	Absolute flow rate	.457	.72	.396

a single line. This is determined by evaluating the F ratio obtained from such an analysis. This technique was used to test whether egg size, male age, and rearing position within a trough influenced dry weight values of sampled fry. It was found that 3-year-old males significantly increased the growth rates of the fry they fathered, $F = 4.4 > F_{.001}\ (5, 1{,}828) = 4.10$, that larger eggs produced larger fry, $F = 15.2521 \quad F > .001\ (40, 1782) = 1.84$, and that rearing position also influenced fry growth, $F = 198.7619 \quad F > .001\ (10, 1818) = 2.96$.

The above findings on the influence of egg size, rearing position within a trough, and fry density during rearing, will be used to refine additional rearing experiments designed to examine the influence of male age on fry growth patterns.

Further replications of the discussed experiments are presently underway at Big Beef Creek. The results from these new experiments and additional data dealing with previously reported studies on redd superimposition and the effects of various gravel depths over impoverished spawning substrates on chum salmon fry survival and quality will be discussed in the Final Report.

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