Title

Chinook Salmon Spawning Behavior: Evidence for Size-Dependent Male Spawning Success and Female Mate Choice

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CHINOOK SALMON SPAWNING BEHAVIOR: EVIDENCE FOR SIZE-DEPENDENT MALE SPAWNING SUCCESS AND FEMALE MATE CHOICE

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by

Randall D. Baxter

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ABSTRACT

The spawning behavior of unmanipulated groups of tagged and untagged chinook salmon was observed during three spawning seasons on Bogus Creek, Siskiyou County, California. Individually recognizable male and female chinook salmon were observed daily throughout their lives on the spawning grounds. Male chinook salmon were observed to compete for access to females. Larger than average sized males were observed to be in primary (dominant) status with females much more often (44 percent of observations) than smaller males (8 percent). In 35 observed spawnings, primary males always appeared to spawn, and entered the nest first or at the same time as the first satellite male in 27 of the 29 spawnings involving more than one male. Individual large males were observed to spawn as a primary male on three occasions , and may have spawned as a primary male on up to 12 occasions.

Female chinook salmon exhibited significantly more aggressive behavior toward smaller males and more courting behavior toward equal sized and larger males. All females spawned in a single redd and almost all females (98 percent) were able to protect their redd from re-excavation by other females to within less than two days of death. The mean lengths of time females occupied their redd were 7.6 days and 8.8 days during 1984 and 1985, respectively.

Based upon behavioral observations in this study and on published literature for other salmonids, it appears that large, dominant male chinook salmon have a reproductive advantage on the spawning grounds. Thus, the reproductive behavior of male chinook salmon may in part counteract any potential for genetic changes in stock specific maturity schedules due to younger aged male spawners. No such advantage was determined for large female chinook salmon in this study, however. Further study on the fertilization success of primary and satellite males, and on how female size relates to redd site selection, nest depth and redd defence is recommended.

ACKNOWLEDGEMENTS

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I would like to thank Dr. David Hankin for selecting me for this project, and for his enthusiasm and perseverance through many manuscript drafts. His guidance and comments contributed substantially to the quality of this project and thesis. I would also like to thank my wife, Jill, for her patience, assistance and encouragement throughout this long process.

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INTRODUCTION

Over the past sixty years the average weight of chinook salmon (*Oncorhynchus tshawytscha*) caught in offshore and terminal fisheries from California to Alaska has declined by more than half and the average age at maturity has decreased by more than one year (Ricker 1980, 1981). According to Ricker (1981) the most important reason for this decline has been:

> ...because non-maturing individuals are taken by the troll fishery; hence, individuals that mature at older ages are harvested more intensively which decreases the percentage of older ones both directly and cumulatively, because spawners include an excess of younger fish.

Hatchery breeding experiments have shown that age at maturity is an inherited trait in chinook salmon (Donaldson and Menasveta 1961, Donaldson 1970, Reimers 1978, Evenson et al. 1980, Hard et al. 1985). If salmon spawn at random on the spawning grounds, then a continued, fishery-induced shift toward younger fish in spawning runs could cause a genetic reduction in stock-specific age at maturity. The long-term result of such a shift would be fewer age classes in the ocean for fisheries to exploit, leading to a possible loss of stability for the fishery as the buffering effects of the older age groups are lost.

The effect of this trend toward younger spawners depends in part upon the relative success of large and small individuals in passing their genes to future generations. If larger individuals have a reproductive advantage on the spawning grounds, then their genes will be passed on to the next generation in greater proportion than their relative frequency among spawners. Such an advantage could come about if reproductive success among males is size dependent, because older males are usually larger. The effects of such size-dependent mating success would be enhanced if females exhibit a preference for larger males.

Rutter (1902), Hobbs (1937), Briggs (1953), and Vronskiy (1972) provided accounts of chinook salmon spawning behavior. Each author observed that males competed for access to females, but no author provided a quantitative treatment of male success by size nor any evidence of females "choosing" mates based upon size. It has, therefore, not been determined whether male reproductive success is size-dependent in chinook salmon.

Male chinook salmon mature and return to their natal streams to spawn at two through seven years of age, creating a situation where the size difference between age two (jack) males and age five to seven males can exceed 50 cm fork length. Thus, if male reproductive success is size dependent in chinook salmon, success of large and small male chinook salmon could be considerably different.

Quantitative descriptions of size-dependent male behavioral dominance and spawning success have been presented for other salmonid species: Atlantic salmon (*Salmo salar*) - Hutchings and Myers 1988; chum salmon (*Oncorhynchus keta*) - Chebanov 1979, Schroder 1981a and 1981b; coho salmon (*O. kisutch*) - Gross 1985; dolly varden (*Salvelinus malma*) - Maekawa and Hino 1986; pink salmon (*O. gorbousch*) - Chebanov 1980, 1982, Keenleyside and Dupuis 1988; and sockeye salmon (*O. nerka*) - Hanson and Smith 1967, Chebanov et al. 1984, Semenchenko 1986, 1987. Spawning success was assessed either by indices of spawning behavior (e.g. movements between females, number of observations with females) or by determination of parentage through electrophoresis. In general, larger males moved less on the spawning ground in search of mates (Hanson and Smith 1967, Chebanov 1979, 1980, 1982), were more often in the company of females (Hanson and Smith 1967, Chebanov 1979, 1980, Schroder 1981a), appeared to dominate smaller males (Hanson and Smith 1967, Schroder 1981a, 1981b, Chebanov 1982, Gross 1985, Hutchings and Myers 1988, Keenleyside and Dupuis 1988), and died with proportionally less gametic material than smaller males (Chebanov 1979, 1982). Residual gametic material also was influenced by sex ratio; small males died with less residual gametic material when females predominated on the spawning grounds, than when males predominated (Chebanov 1982).

In cases where electrophoretic analysis was used to establish parentage after spawning (Schroder 1981a, Chebanov et al. 1984, Hutchings and Myers 1988), observations of behavioral dominance among spawning males were reflected in corresponding greater number of fertilizations by the dominant male. Schroder (1981a - chum salmon) observed complete exclusion of subordinate males in four of ten trials, and no fertilizations in another instance where the subordinate entered the nest and spawned. Yet, the contribution of subordinate ("sneaker", Gross 1985) males was not inconsequential in the remaining five spawnings and was estimated to range between 17 and 46 percent in individual spawnings (Schroder 1981a). The success of sneaker males depended on their proximity to the redd, and their ability to perceive that spawning commenced, then move in and release milt while eggs remained to be fertilized (Schroder 1981a). These studies demonstrated that behavioral dominance among males gave dominant males a competitive advantage in obtaining fertilizations. Furthermore, male size and, to a lesser extent, male energy were the operative factors influencing male dominance (Schroder 1981a, Chebanov et al. 1984).

Observations of female salmonids on nests have suggested that females prefer larger males (Hanson and Smith 1967, Schroder 1981a, 1981b, Semenchenko 1987). Schroder (1981a, 1981b) found that females presented with only "small" males slowed down their nest construction compared to when they were only courted by larger males.

Similarly, Semenchenko (1987) observed that the duration of female sockeye salmon spawning (time on the redd) was extended when only "small" males were present. Schroder (1981a) suggested that by slowing nest construction the female increased her chances of being found by a larger male and in this way attempted to "select" a mate. Hanson and Smith (1967) observed that female sockeye salmon attacked small males more than large ones. Thus, female behavior also affected male spawning success.

If chinook salmon spawning behaviors and responses are similar to those observed in spawning behavior studies of other salmonids, then older, larger males may have greater spawning success than smaller, younger males, and females also may prefer larger males as mates. If this is the case, then behavior of chinook salmon on the spawning grounds may help buffer potential genetic shifts toward younger age at maturity that might otherwise result from fishery-induced shifts toward younger-aged fish in the spawning runs.

The spawning behavior of unmanipulated groups of tagged and non-tagged chinook salmon was observed during three spawning seasons. The objectives of this study were to: 1) describe chinook salmon spawning behavior as a basis for understanding their reproductive ecology; 2) determine whether male chinook salmon competed for females and whether male size influenced the apparent outcome of the competition; and 3) determine whether females exhibited behavioral evidence of "choosing" males based upon the relative size of the male.

STUDY AREA

Bogus Creek is the first salmonid spawning tributary entering the Klamath River below Iron Gate Dam (Siskiyou County, Northern California). It flows adjacent to Iron Gate Fish Hatchery before entering the Klamath River approximately 316 km upstream of the Pacific Ocean (Figure 1). Bogus Creek is a second order stream which drains about 142 square km of volcanic soils in the semi-arid, southern Cascade Mountain Range.

Minimum flows during late September 1984 and 1985 were 0.34 and 0.42 cubic m per second (12 and 15 cfs), respectively. These flows were sufficient to allow chinook salmon to enter the creek, but cessation of irrigation upstream (or rain) by early October appeared necessary for salmon to access all available spawning areas (in particular, the Cold Creek area). Areas used for spawning by chinook salmon included the first 7.2 km (out of 24.2 km) in Bogus Creek, and about 0.8 km (out of 8.5 km) in Cold Creek (Figure 1).

An adult salmonid counting weir is located approximately 460 m from the mouth of Bogus Creek (Figure 2). California Fish and Game counts of chinook salmon migrating past this structure averaged 3,923 adults and 1,082 jacks per spawning season from 1978 through 1983 (jacks, usually less

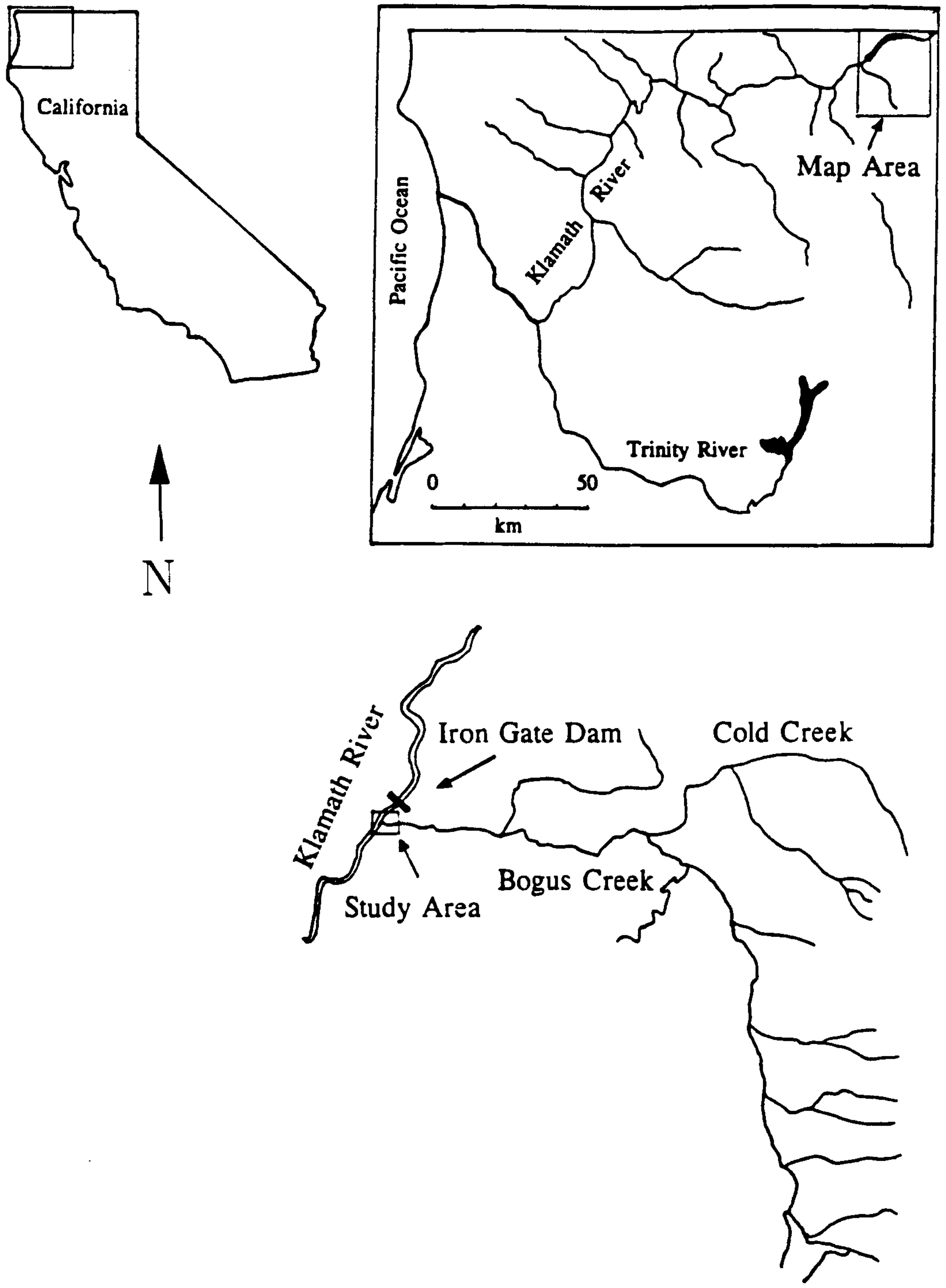


Figure 1. Klamath Drainage, Bogus Creek Drainage and Study Area Location in Northern California.

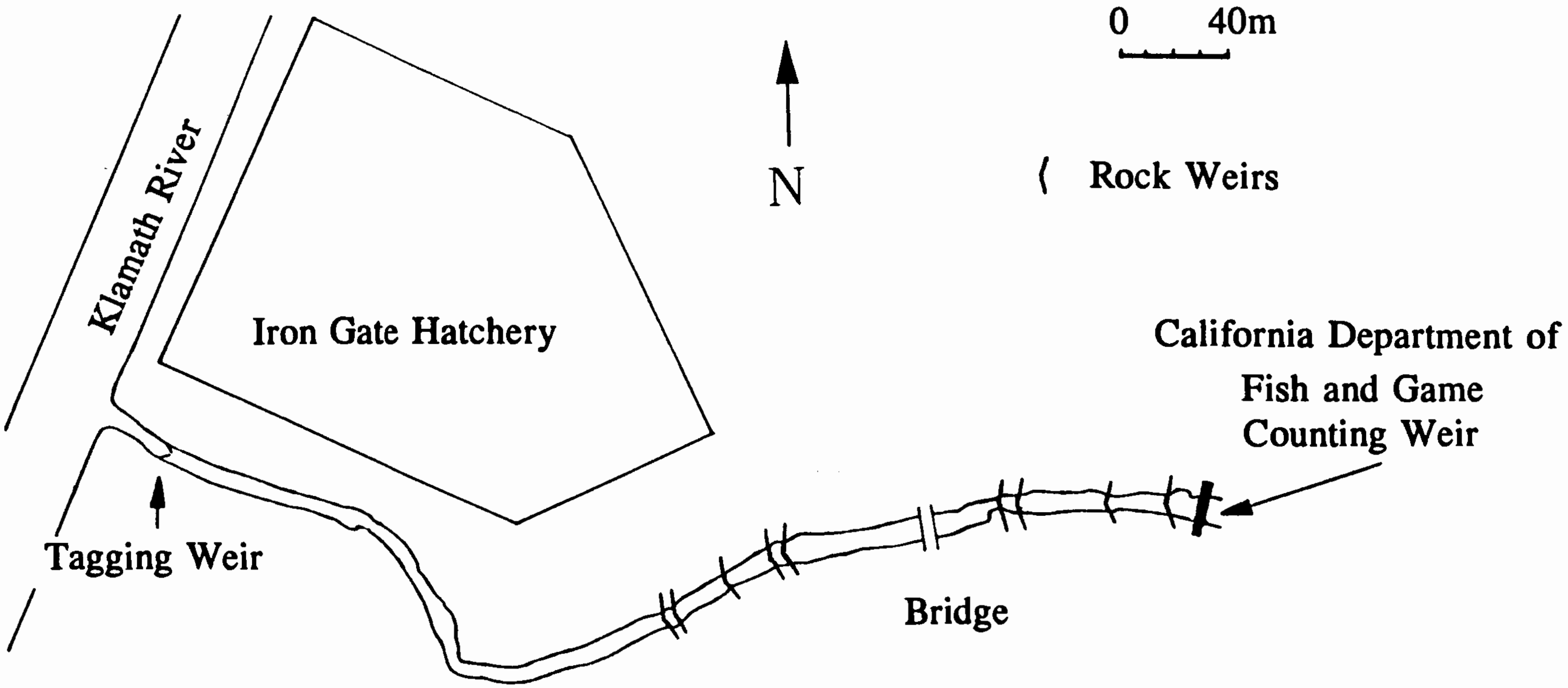


Figure 2. Bogus Creek Study Area Including Locations of the Study Tagging Weir and the California Fish and Game Salmon Counting Weir.

than 55 cm fork length, were separated from adult males based upon size). Chinook salmon enter the stream from about the second week in September through the first week in November, with about 80 percent of the run entering during the first three weeks in October. The peak of spawning activity follows the peak of migration by only two to four days in the lower km of Bogus Creek and by a week or more in the Cold Creek area.

The study area was limited to the lower 460 m of the creek: from the mouth of Bogus Creek upstream to the California Department of Fish and Game Counting Weir (Figure 2). Stream gradient within the study area averaged 1.2 percent; most of this gradient was accounted for by short drops associated with introduced rock weirs. Creek width (wetted perimeter) averaged 6.25 m ± 1.43 m (Standard Deviation). Extensive spawning gravels were located throughout the study area. Water depth over spawning gravels generally ranged from 0.09 m to 0.34 m, but was occasionally as deep as 0.58 m.

High banks lined both sides of the stream and provided good vantage points for observation. Cover provided by riparian vegetation allowed observations of spawning chinook salmon from within 10 m of the subjects. Large numbers of early-spawning chinook salmon, easy access and good weather during the spawning period made lower Bogus Creek an excellent location for observing chinook salmon spawning behavior.

MATERIALS AND METHODS

Observations on chinook salmon spawning in Bogus Creek were conducted during the Fall of 1983, 1984 and 1985. In 1983, field work was of a preliminary nature and was limited to the first three weekends in October. This work resulted in definitions of behaviors to be recorded and a decision to use modified focal-animal sampling (Altmann 1974) as a method for collecting behavior data in subsequent observations.

Five tasks were undertaken during each of the two primary study years (1984 and 1985): 1) study area mapping; 2) salmon trapping and tagging; 3) weir monitoring; 4) behavior observations; and 5) carcass surveys. Unless otherwise stated, techniques used to accomplish each task were identical for both years.

Chinook salmon were measured and tagged as they entered Bogus Creek, allowing positive identification of individual fish and providing a size reference for length estimation of untagged chinook salmon. The California Department of Fish and Game counting weir (counting weir) was monitored to record the number of study-tagged chinook salmon which moved upstream of the study area and to record the length frequency of chinook salmon that migrated past the weir. Daily locations of identified male and female chinook salmon were plotted on scale maps of the study area to follow fish movements. Behavior observations were conducted to determine if males competed for females, if females used behavior to select their mates, and if apparent spawning success of different males was related to male size. Carcass surveys were conducted to establish dates of death for individual chinook salmon, thus allowing their time on the spawning gravels to be calculated. Carcass recovery locations were noted to determine if size or sex influenced the likelihood that a carcass would be recovered in Bogus Creek or washed into the Klamath River.

Study Area Mapping

In 1984, mapping involved measuring 10 m intervals following the center of the channel from the mouth of Bogus Creek upstream to the counting weir. A surveyor compass was used to obtain the direction of the mid-channel line between the end points of each 10 m interval. At each interval end point the wetted surface width was measured and recorded in meters. Streamside landmarks were added to the scale map produced by these measurements.

In 1985, mapping techniques were the same except that a level and stadia rod were used to obtain elevations and more accurate distance and azimuth information. Water depth was measured to the nearest 0.03 m mid channel with the stadia rod. Color-coded, wooden stakes were pounded into the lower bank at the end points of each 10 m interval and allowed the locations of fish and redds to be accurately recorded on the map produced from these data.

Trapping and Tagging

The salmon trap and tagging weir was located approximately 25 m from the mouth of Bogus Creek in an area of slower water, 0.24 m deep (Figure 3). In 1984, the trap was fished three days per week (Thursday AM to Saturday PM) during calendar weeks 38 and 42, and two days per week (Thursday AM to Friday PM) during calendar weeks 39, 40 and 41. All non-morbid chinook salmon trapped entering Bogus Creek for the first time were tagged.

In 1985, the trap was fished on Tuesdays and Wednesdays during calendar weeks 39 through 41 and on Tuesday of calendar week 42. Male chinook salmon less than or equal to 55 cm fork length during 1984 and less than or equal to 60 cm during 1985 were considered jacks based on California Department of Fish and Game length cut-offs for those years (I. Paulson, pers. comm).

Trapped chinook salmon were netted, placed into a cradle, measured to the nearest cm fork length, sexed, tagged with Peterson discs, and released upstream of the trap and weir. Peterson discs were 3.2 cm diameter, color-coded and numbered. Males were tagged ahead of their dorsal fin and females behind the dorsal fin. In 1985,

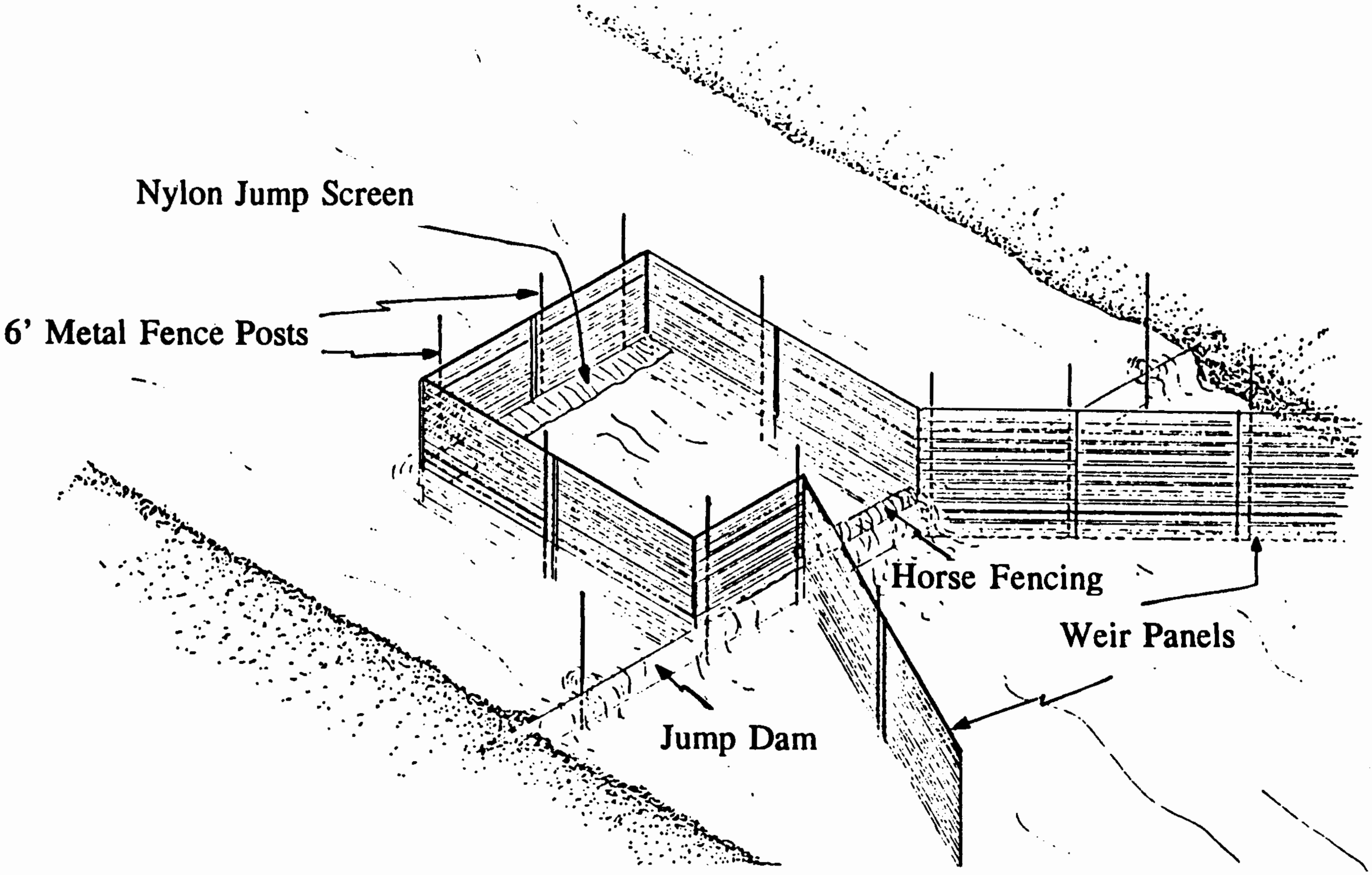


Figure 3. Salmon Weir and Trap Used to Capture Chinook Salmon for Tagging. Six Foot Metal Fence Posts Were Used to Support a Jump Dam (Three Pieces of Plywood Measuring 0.25 m x 0.019 m x 24.4 m) and Twelve Metal Weir Panels (1.22 m High by 1.52 m Long) Which Comprised the Trap and Weir. A 2.44 m x 0.3 m Piece of Nylon Fabric Was Attached at Water Level on the Upstream Side of the Trap and 0.61 x 1.07 m Piece of Horse Fencing Was Attached to Strain Water Spilling out of the Trap Opening. All Attachments Were Made Using Bailing Wire.

postorbital to hypural plate (POHP) length measurements (Vladykov 1962) also were taken from length-stratified samples of both sexes.

Salmon Counting Weir Operation

Chinook salmon run monitoring lasted from 12 September through 28 October 1984 and from 16 September through 4 November 1985. During these periods, virtually every adult salmonid which passed the California Department of Fish and Game counting weir was identified to species, sexed, checked for marks or tags and released upstream. During each study year, a sample of the chinook salmon were measured to the nearest cm fork length. Fish were checked and passed above the weir from dawn to dark seven days a week.

Behavior Observations

Behavior observations fell into two categories: 1) long-term (10 or 20 min in duration) and 2) short-term (less than two min in duration) Focal-Animal (Altmann 1974) samples. Observations were generally conducted independently by two observers. Observers conducted simultaneous observations of the same chinook salmon at the start of each season to standardize techniques for defining and recording behaviors, and for estimating fish lengths.

Observers wore polarized sun-glasses during behavior observations. Binoculars (7 x 35) were carried to assist in reading Peterson-disc tag-numbers at a distance, but were not necessary for behavior observations. Peterson discs numbers, darkened with a black permanent marker, were identifiable at distances of at least 5 m; binoculars increased this distance to about 15 m for fish in shallow (< 0.40 m) water. These distances applied when visibility in the water was at least 0.30 m.

Increased turbidity after rains reduced visibility in the water from over 0.60 m to less than 0.15 m during three days in 1984 (11 and 17 October, and 2 November); no long-term behavior observations were conducted during these days. In 1985, turbidity precluded behavior observations on 27 and 28 September, and 3 and 21 October. Otherwise, water visibility in 1985 varied between 0.30 m and 0.60 m and was adequate for behavior observations.

Study Area Surveys and Spot-Sampling

Study area surveys involved one or both observers walking the southern stream bank from the mouth of Bogus Creek upstream to the counting weir and recording locations of all early (before 2 October) redds (Table 1), locations and descriptions of all females observed starting a redd , and locations of tagged or "known" fish (previously observed, non-tagged chinook salmon distinguishable from

Table 1. Definitions of Terms Used in Descriptive Text and Analyses. Synonymous Terms and Their Citation Are Included in Parentheses.

Primary male (Alpha male, Schroder 1981a). The courting male closest to the female; other males may or may not have been present (Keenleyside and Dupuis 1988). This male repulsed attempts by other males to court the female and was considered dominant when other males were present.

Jack (grilse, Briggs 1953). Precociously maturing male salmon which returns to spawn at age 2 yr (Beacham and Murray 1985).

Nest (egg pocket, Hobbs 1937; pot, Burner 1951; bed, Jones and Ball 1954; or redd, Vronskiy 1972). The depression a female excavated in the gravel in which she eventually deposited her eggs (Tautz and Groot 1975).

Redd. The contiguous area of gravel disturbed by a female as she excavated all her nests. Collective term for all nests and tailings (Hobbs 1937, Burner 1951).

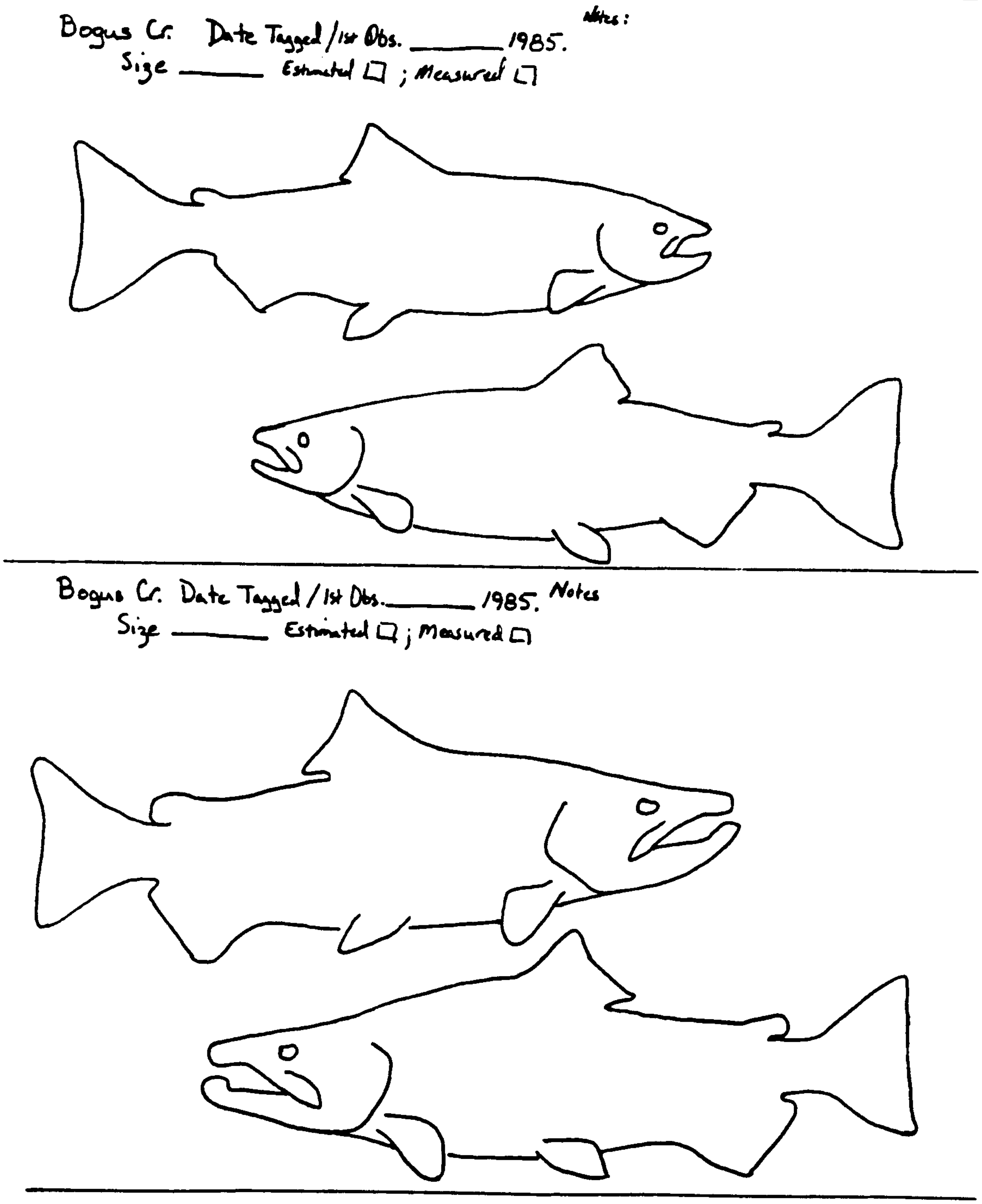
Satellite male. Any male on the periphery of a redd occupied by a female and primary male that attempted to court the female, or maintain a position close to the female when faced with aggression from the female or primary male (Schroder 1981a, Keenleyside and Dupuis 1988). Satellite males were referred to based upon their proximity to the nest; the first satellite male was closest to the nest, the second satellite male was next closest and so on.

others by the combination of length, coloration and scars) on a survey map. Surveys were conducted daily at approximately noon in 1984. In 1985, surveys were conducted twice daily at approximately eight AM and four PM.

Bogus Creek water temperatures (°C) were measured at approximately eight AM and four PM on a daily basis. These temperatures were treated as daily minima and maxima, and readings for the entire season were used to produce an average daily water temperature for the spawning period of each year.

During study area surveys any tagged or known chinook salmon seen were "Spot-Sampled" immediately. Spot samples were short duration (less than 2 min) focal-animal observations (Altmann 1974). Data recorded included relative size and apparent sex of any interacting fish, the first behavior(s) of the spot-sampled fish during this period, date, time and location. These data were recorded on individual fish profile cards (Figure 4). Diagrams of marks and scars present on the fish were updated at each observation. Fork length and sex (all fish), and tag number and date tagged (tagged fish) were recorded on each card for identification.

Profile cards were made for all tagged chinook salmon observed in the study area on two or more consecutive surveys. Profile cards were made for non-



Bogus Cr. Date Tagged/1st Obs. ______ 1985. Notes:
Size ______ Estimated ☐ ; Measured ☐

Bogus Cr. Date Tagged / 1st Obs. ______ 1985. Notes
Size ______ Estimated ☐ ; Measured ☐

Figure 4. Examples of Fish Profile Cards Used to Record Spot Sample Data for Male and Female Chinook Salmon under Observation in Bogus Creek during 1984 and 1985.

tagged females observed initiating a redd on one day and observed on the same redd the next day, and for non-tagged males when the combination of length, coloration and scars insured that the male would be easily recognized. Non-tagged females or males which met the criteria for a profile card and whose spawning behavior data were used in analyses will be described as "known" females or males in subsequent text.

The completeness of all early redds and redds of tagged females was recorded at each survey on the survey map in one of four categories: R-1, newly begun, bottom disturbed but no depression evident; R-2, some depression evident, but not deep enough for spawning; R-3, nest deep enough for spawning; R-4, first nest complete, working on others. For tagged females first observed well into the construction of their first nest, category of redd completion was used to estimate the time of nest initiation.

Daily spot samples were used to estimate the reproductive lifetimes for individuals of each sex. Females were assumed to be reproductive (physiologically able to release ripe eggs) after the initiation of their first nest. Reproductive lifetimes could not be estimated for all females. For all females for which redd initiation date was known and for which spawning was observed, the difference between the two events was calculated in days.

The largest of all such differences was assumed to represent the maximum reproductive period for all females.

Males were assumed to be reproductive (physiologically able to fertilize eggs) when they began exhibiting courting behavior directed at females, or remained in or returned to a satellite position in the face of aggression from a primary male (see Table 1 re definitions of primary and satellite males). Furthermore, these males were assumed to remain reproductive until they were no longer interested in females as indicated by their lack of association with reproductive females. Number of days reproductive for tagged males in 1985 was calculated as the number of 24 hr periods after first courting to the last association with a reproductive female rounded to the nearest 0.5 day.

Female redd defense or territorial behavior was assessed during spot samples by noting the response of each spot sampled female to at least two fish intruding into her redd area. An aggressive response (bite or chase) was recorded as territorial behavior. Females never observed to behave aggressively toward intruding fish were considered non-territorial. A territorial female did not need to express aggressive behavior at every observation; she was assumed to be territorial from the start of her first nest through the last day she exhibited aggressive behavior. The number of days territorial for each tagged or known female (i.e. non-tagged female whose redd initiation date was known) was calculated as the number of 24 hr periods from the time of redd initiation until the last observed territorial behavior, rounded to the nearest 0.5 day.

Possible relationships between fish length and estimates of the number of days alive, for females (1984 and 1985), and the number of days reproductive and alive for tagged males (1985) were examined using non-parametric Spearman rank correlations, r_s (Zar 1974). Mann-Whitney U tests (Zar 1974) were used to determine if differences existed between the number of days alive of females initiating redd construction before and after the mid-point of the spawning period.

Male status in courting groups was noted during spot samples to determine how size affected the ability of a male to attain primary or satellite status (Table 1). Male status during spot samples was recorded in one of four categories: 1) primary ; 2) satellite male; 3) non-courting (with a female, but no courting behavior observed); or 4) alone (wandering or holding alone).

Long-Term Focal-Animal Sampling

Long-term "focal-animal" sampling consisted of 10 (males) or 20 (females) minute, tape-recorded, verbal records of behavior and elapsed time. Behaviors were recorded as events (Altmann 1974). Each record included the sex and relative size of all interacting fish. Focal-animal records were transcribed to paper as soon as possible after the sample ended by the observer who made them (Figure 5). Selection of individuals to be sampled differed between males and females.

Focal-Female Sampling. Individual females were initially selected as candidates for long-term behavioral sampling from among those females (tagged or not) observed starting their first nest during study area surveys. These females were grouped by known or estimated fork length into small (< 70 cm) or large (≥ 70 cm) size classes. Random numbers were generated with a calculator and assigned to each female. Within each size class, females were then ranked by random number in ascending order and were selected for observation based upon their rank. At an assigned time, if a female matching the description of the first ranked female was on or near the redd location recorded, then focal-female sampling commenced; if not, the redd location of the next lowest ranked female within the size group was checked and she became the focal-female if she was identified on the recorded location. This process was continued until a female was located on a recorded location.

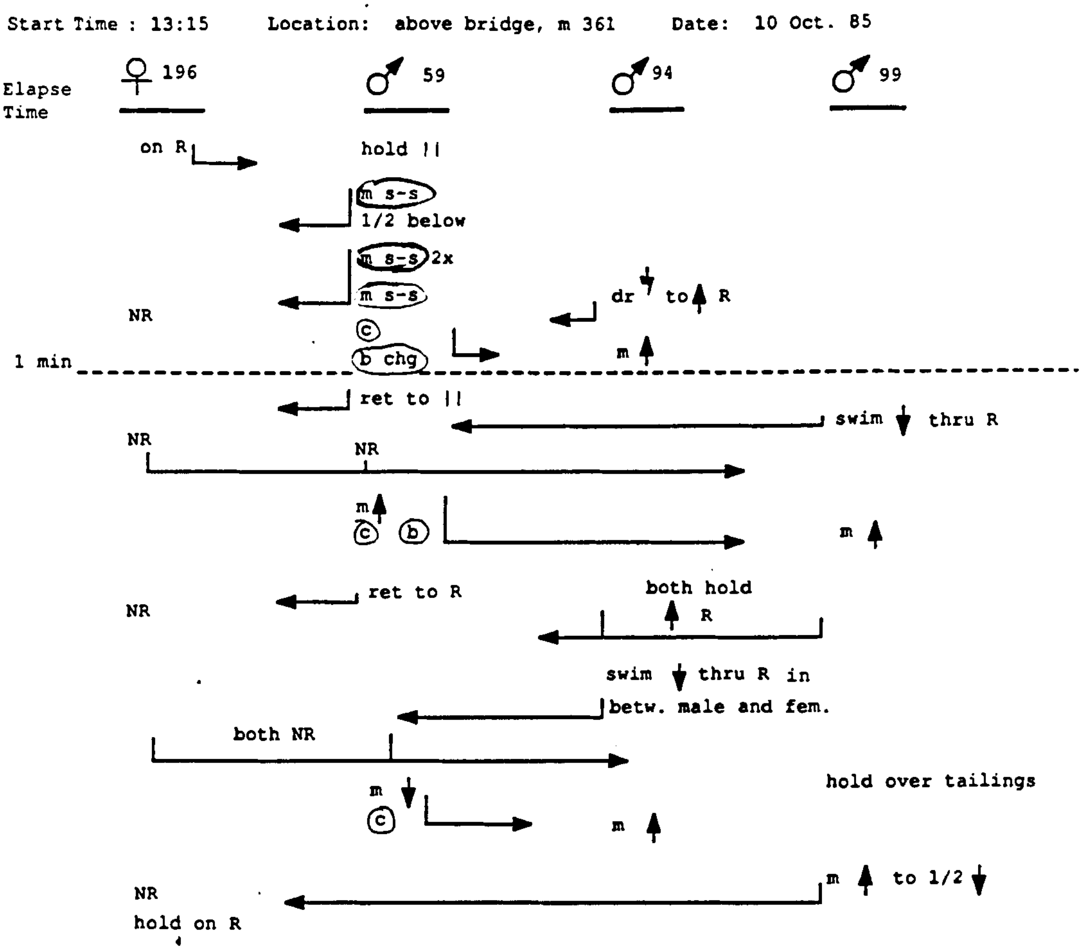


Figure 5. Example of Focal-Animal Transcription Format. Time Scale in Minutes in the First Column; Focal-Female Identification and Her Behaviors in the Second Column from the Left; Identification of the Primary Male and His Behaviors in the Third Column from the Left; and Identifications and Behaviors of Satellite Males Associated with The Pair. All Four Fish in this Example Were Tagged. Behaviors Used in Analyses Were Circled to Assist Summarization. Distance on Sheet Is Not Proportional to Elapsed Time. Behaviors recorded are: b chg = charge bite; c = chase; b = bite; m s-s = move side to side. Arrows indicate the individual at which the behavior(s) were directed.

Once selected as a focal-female, the female was behaviorally sampled on a daily basis for at least three days. New females were selected for observation, as described above, when previously selected females died or were no longer being courted by males.

On a daily basis, each of two observers was randomly assigned to sample the behavior of at least one female from each size group (two females per size group if time allowed). Sampling times were determined by generating a random number ($0 < r < 1$) for each female to be sampled, multiplying by the number of hours between 9 AM and dusk not used for other tasks, then adding the resulting hours to the time selected for the start of the day (9:00 AM). If the female scheduled for observation was located on or near her redd at the assigned time, then sampling commenced; if the scheduled female was not located and no alternates existed (i.e. no new females not already scheduled), observers tried to sample the behavior of any female that appeared close to spawning. Data from such samples were used in analyses only if a spawning was observed.

Focal-female (and male) samples were only analyzed if behavior was undisturbed. Behavior was assumed to have been undisturbed if the observer was able to take a vantage point for sampling and record the entire sample without causing fish in the area to swim for cover.

The initial behavior of unpaired (no primary male present) focal-females toward each new male encountered was assigned to one of two behavior categories (1. chase or bite, Table 2; or 2. any other behavior) for each of three male relative size categories. Two or more new males were usually encountered by each female sampled. Male size was estimated relative to the focal-fish, and assigned to one of three categories: smaller males (those more than 5 cm smaller than the focal-fish); approximately equal sized males (those within 5 cm larger or smaller than the focal-fish); and larger males (those more than 5 cm larger than the focal-fish). Only the first sample, chronologically, in which a female was both reproductive and unpaired was used for this analysis when more than one sample fitting the conditions listed existed for a given female. The resulting frequency tables from unpaired females were combined and chi-square contingency analysis (Snedecor and Cochran 1967, Box et al. 1978) was used to test if initial female aggression was independent of male relative size.

Female behaviors exhibited toward males of different relative size were tallied into three by four frequency tables for each focal-female sample collected during each of the first three days a female spent on her redd. This resulted in separate frequency tables for each focal-female sample. Male relative size categories were as described previously. Female behavior toward males was separated

Table 2. Definitions of Behaviors Used in Descriptive Text and Analyses. Synonymous Behaviors and Their Citation Are Included in Parentheses.

Bite. When the actor made open-mouth to body contact with another fish. The actor may or may not have closed down on the other fish (Kalleberg 1958, Hanson and Smith 1967).

Charge-Bite. When the actor swam rapidly toward an opponent and directed a bite to the head or mid-section of the opponent, who made no attempt to avoid contact (Jones and Ball 1954).

Chase. Rapid movement or swimming by the actor in the direction of another fish. This behavior was recorded when the actor moved more than one body length in the direction of another fish (Kalleberg 1958, Hanson and Smith 1967).

Dig (cutting, Jones and Ball 1954). A contiguous series of strong body flexures performed by a female while turned on her side over the gravel, and used to excavate or fill-in a nest (Tautz and Groot 1975).

Move Parallel (parallel, Berst et al. 1981). The actor moved to a position alongside another fish so that both fish were side by side and head to head.

Move side to side (cross-over, Tautz and Groot 1975, Berst et al. 1981). A single or contiguous series of movements in which a male, positioned with his head alongside the female between her dorsal fin and tail, swam over her back and tail to the same position on her opposite side. A non-broken series of these movements was considered one behavior.

No Reaction. When a behavior expressed toward a focal fish did not elicit an overt response within approximately five seconds.

Nudge. When the actor used its snout, mouth closed, to make gentle contact with another fish (Needham and Taft 1934).

Push (back-pedalling, Hanson and Smith 1967; tail flick, Newcombe and Hartman 1980). Contact between two fish in which the actor moved its body (tail or side) into the other fish. The actor used the current to carry it downstream into the other fish or swam close in front of the other fish, then turned and used its tail to "push" the other fish.

Table 2. Definitions of Behaviors Used in Descriptive Text and Analyses. Synonymous Behaviors and Their Citation Are Included in Parentheses. (continued)

Quiver. While alongside a female or a fish acting like a female, a male erected his dorsal fin and produced high frequency, low amplitude body undulations; the male appeared to vibrate (Jones and Ball 1954, Tautz and Groot 1975).

Spawning. The female moved into a test posture in her nest, one or more males moved parallel, tilted slightly away from the female and all participants arched their backs, erected their dorsal fins, and opened their mouths while releasing gametes. Immediately after a true spawning the female moved to the upstream edge of her nest and dug alternately on one side then the other, causing gravel to fill in the nest (McCart 1969, Tautz and Groot 1975). An increased rate of digging and digging alternated between upstream edges of the nest were used as evidence of female release of eggs (see, McCart 1969, Tautz and Groot 1975).

Spawning, False. Female behavior appeared the same as during a true spawning and males released gametes; however, the female did not immediately begin filling the nest afterward (McCart 1969, Tautz and Groot 1975). The female continued to periodically test or dig through the center of the nest. This indicated the female had not released gametes.

T-Display. A male, positioned upstream of another fish with his dorsal fin erected, presented a lateral body view to the other fish. The displaying male glided across upstream and in front of the other fish, then turned and repeated the action moving laterally in the opposite direction (Schroder 1981a).

Test (crouch or feel, Jones and Ball 1954; probe, Tautz and Groot 1975;). A female salmonid "tested" by resting her tail on the up-slope of the downstream end of the depression, arching her back and extending her anal fin down into the gravel. She may or may not have opened her mouth during the test. Females also moved laterally through their nest while in this posture, probing the bottom with their anal fin.

into four categories: 1) dig, 2) nudge or move parallel, 3) chase or bite, and 4) no reaction (Table 2).

Female behavior toward males of different relative size was analyzed separately for each day of the first three days females spent on their redds. Behavioral frequency data summarized from focal-female samples collected during the first day females spent on their redd were combined for analysis of behavior during day one. Likewise, frequency data from focal-female samples collected during the second and third days females spent on their redd were combined with other data from days two and three, respectively, and analyzed separately. Only data from one focal-female sample for each female was used in the analysis for a given day. No focal-female samples which included a spawning were used in these analyses.

Although some females only interacted with only one male or with males of a single size group during 20-minute focal-female samples, each female probably encountered males of all sizes during her spawning period. Furthermore, inter-female similarity in behavioral response toward males of different relative size was assumed for females at the same stage of their reproductive period, and interacting with the same number and combination of different sized males. Given these assumptions, focal-female samples collected from different females during the same day after redd initiation could be legitimately combined. These assumptions could not be tested using unmanipulated groups of reproductive chinook salmon.

The number of males interacting with a female was calculated as an average of the number of individual males interacting with a female during focal-female samples collected in 1984. Focal-female samples from 1984 also were used to determine female digging rates during non-spawning observations (digs/min averaged over 20 min) and the number of bite exchanges per female-female aggressive interaction. All samples taken during the first three days each tagged or known female spent on her redd were used for these calculations.

Focal-Male Sampling. In 1985, 10 minute focal-male samples were conducted on tagged males within the study area. At a random sampling time and location within the study area the first tagged male found upstream of the selected location was observed. Sampling time was randomized the same as for female. The location to begin a search was randomized by generating a random number ($0 < r < 1$) and multiplying by the study area length (460 m). Two to four focal-male samples per observer per day were attempted. An individual male was sampled at most once by each observer during a given day.

Focal-male samples from 1985 were summarized into frequencies of male behavior toward other males of different size relative to the size of focal-males. Male behaviors toward other males were assigned to one of five categories: 1) swim away or drift downstream (i.e. moving away from the other male), 2) chase or bite, 3) T-display, 4) nudge or push, or 5) no reaction (Table 2). Behavior samples in which the focal-males were in primary or satellite positions for at least seven of the 10 minutes were used for this analysis. Only the first sample, chronologically, of each male that met the criteria was used in the analysis.

Observed Spawnings. All focal-animal samples which included a spawning were treated as comparable in terms of male and female behavior. When fish behavior and redd-stage indicated that spawning was imminent, observers initiated focal-female sampling regardless of whether the reproductive history of the female was known. Focal-female (and male) samples from fish of known and unknown reproductive history were used to determine how females and primary males behaved immediately prior to and after spawning.

When spawnings were observed with little or no warning, data collected included date, time, estimated or known female length, relative, estimated or known size of all males in the courting group, the number of males in attendance, the number entering the nest at the time of spawning and their rank order of entry. Complete records were not obtained for every spawning observed.

Male spawning success was estimated in two ways. First, all undisturbed spawnings were categorized based upon the number of males in the courting group. For each category of two or more males, the proportion of total spawnings in which the primary male entered the nest before, at the same time as or just after the first satellite male at spawning were calculated to determine if primary status resulted in early entry into redds at spawning.

Second, a minimum total number of spawnings was estimated for each tagged male in 1985 as the sum of actual spawnings observed and the number of observations in which the male was with a reproductive female whose behavior indicated imminent or recent spawning. When a tagged male and the same reproductive female were observed together during consecutive observations over an eight hr period (the length of time between consecutive spawnings of one known female) another spawning was added to the sum.

Carcass Surveys

Carcass surveys were conducted on a daily basis from 16 September to 2 November 1984, except for 27-29 October, and covered the entire study area. Every dead chinook salmon located was inspected. Data recorded were sex, jack or adult for males, tags or marks, and a subjective estimate of time since death (fresh mortality, 1 day old or old mortality). Postorbital to hypural plate (POHP) length measurements were taken from carcasses that showed distinctive scars of lost disc tags. Positive identifications of all fish that had lost tags were made based on fish size (POHP - fork length relationships), location at death and identifying scars.

After exterior inspection, carcasses were cut in half with a machete to prevent recount on subsequent surveys. Sex products retained at death were recorded in one of three categories: 1) most or all (prespawning mortality); 2) some (partially spent); or 3) little or none (spent).

In 1985, the tagging weir was left in the stream on non-tagging days and used to retain carcasses and morbid fish that otherwise would have floated out of Bogus Creek. Carcass counts were conducted every two days from 1 to 28 October by project personnel and on 4 and 11 November 1985 by Fish and Game personnel. Data recorded were the same as for 1984, except that carcasses recovered on the tagging weir were separated from those recovered upstream. In November 1985, carcass counts did not distinguish carcasses collected on the tagging weir from those counted upstream, or prespawning mortalities from spent carcasses.

RESULTS

Characterization of the Spawning Run

Chinook salmon were larger and more abundant in 1985 than in 1984 (Table 3). Jack chinook salmon comprised about 15 percent and about 30 percent of the run in 1984 and 1985, respectively. Timings of migration for adult males, females and jacks were similar for both years (Figure 6). Adult males and females entered Bogus Creek in approximately equal numbers at about the same time, whereas jacks entered later and, in 1985, outnumbered adult males during the latter portion of the run (Figure 6). All means reported in the text are followed by standard deviations and sample size in the form: mean ± standard deviation (sample size).

Fish Tagging

During 1984 and 1985, 163 and 286 chinook salmon, respectively, were trapped and tagged as they entered Bogus Creek. In 1984 and 1985, tagged males larger than 72 cm in length spawned and died in the study area in proportionally higher numbers than smaller males (Figure 7). In 1984, 17 of 79 (22 percent) tagged males remained in the study area, including 1 of 6 (17 percent) tagged jacks ($\leq$ 55 cm), 12 of 59 (20 percent) tagged males between 56 and 72 cm, and 4 of

Table 3. Total Counts, Number Measured, Mean, Standard Deviation (S.D.) and Range of Fork Lengths (cm) by Sex and Year of Return for Chinook Salmon Passing The Bogus Creek Counting Weir. Upper Limits of Jack Size Were 55 cm FL in 1984 and 60 cm FL in 1985.

Year of Return	Sex	Total Number	Number Measured	Mean Length	S.D.	Range
1984	Male	756	474	67.95	7.38	56 - 94
	Jack	263	131	47.59	4.78	30 - 55
	Female	783	498	67.07	5.79	43 - 84
1985	Male	1214	585	77.73	8.80	61 - 99
	Jack	1132	383	53.92	4.61	35 - 60
	Female	1387	689	75.49	6.48	40 - 94

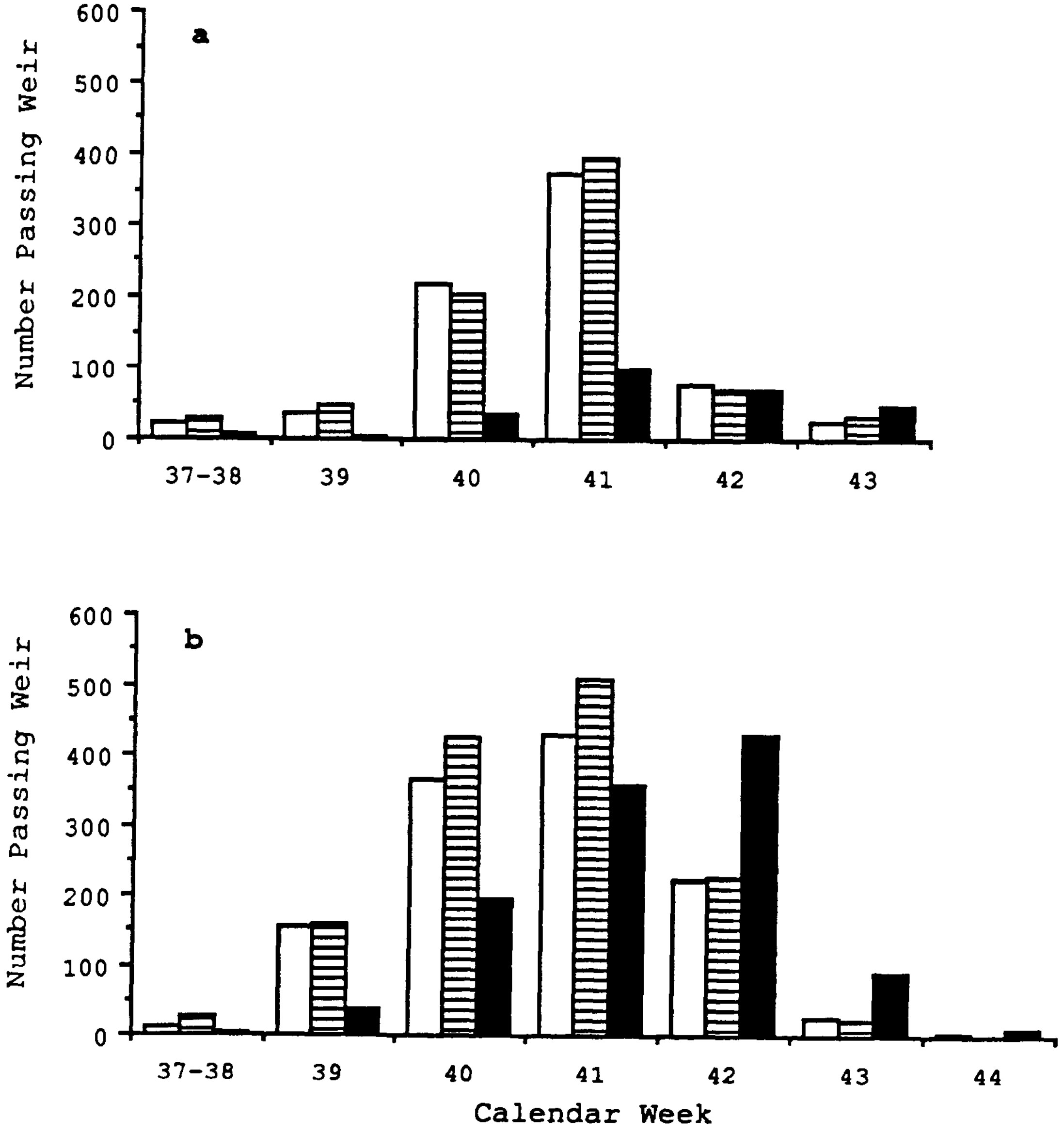


Figure 6. Counts, by Calendar Week, of Adult Male (White Bar), Female (Hatched Bar) and Jack (Black Bar) Chinook Salmon Passing Bogus Creek Counting Weir during 1984(a) and 1985(b).

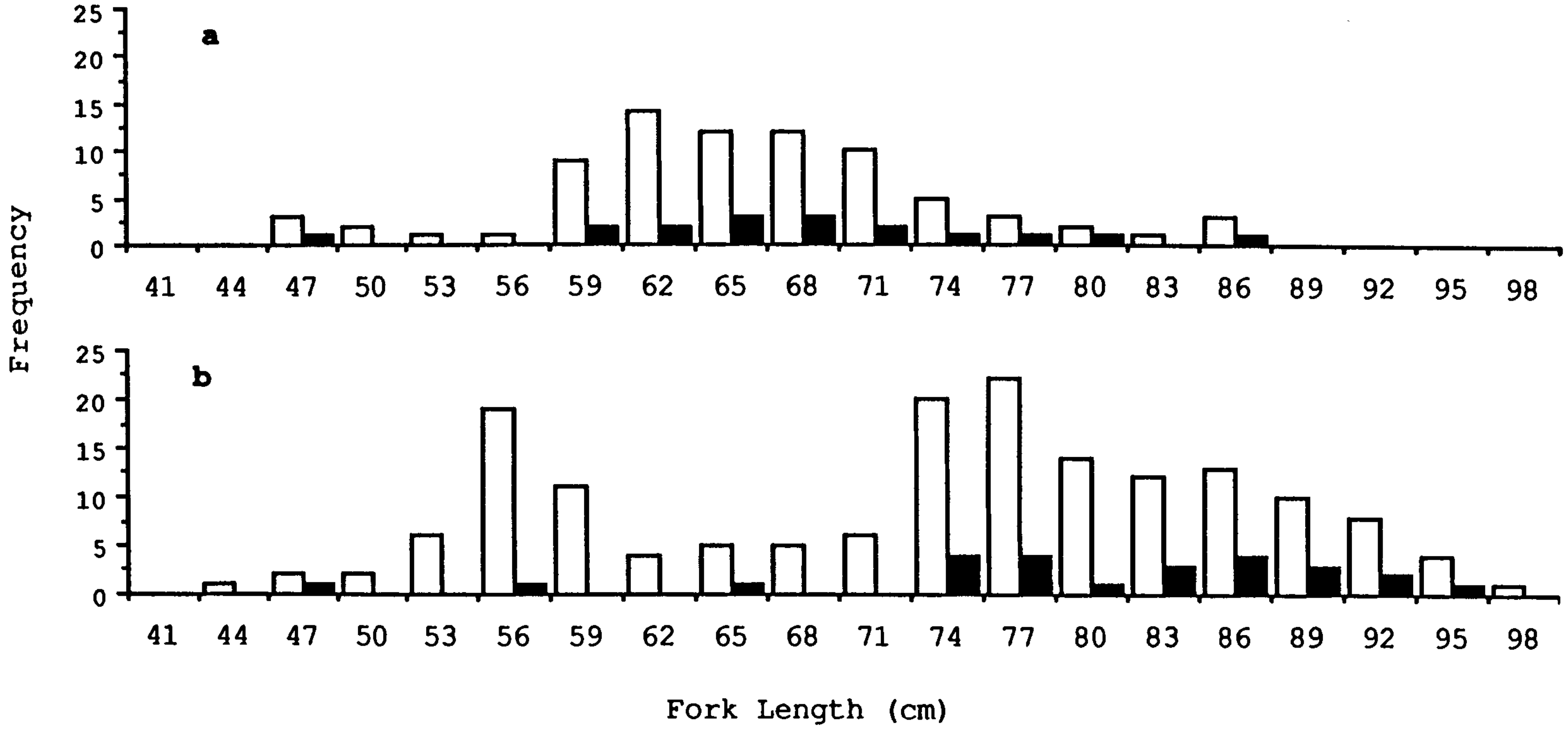


Figure 7. Length Frequency of All Tagged Male Chinook Salmon (White Bars) and of Males Remaining in the Study Area through Spawning and Death (Black Bars) in 1984(a) and 1985(b).

14 (29 percent) males larger than 72 cm. In 1985, 25 of 164 (15 percent) tagged males remained within the study area; however, this included only 2 of 41 (5 percent) jacks (≤ 60 cm) and 1 of 20 (5 percent) tagged males in the 61-72 cm size category, whereas 22 of 103 (21 percent) tagged males larger than 72 cm remained within the study area (Figure 7).

Tagged females remained within the study area in higher proportions than males during both years (Figures 7 and 8). In 1984, 32 of 84 (38 percent) tagged females remained in the study area. These females were distributed throughout the range of female lengths. In 1985, 39 of 122 (32 percent) tagged females remained within the study area. Of the smaller than average females (< 75 cm, Table 3) only 9 of 42 (21 percent) remained, whereas 30 of 80 (38 percent) tagged females of 75 cm or larger remained within the study area (Figure 8).

Behavior of Chinook Salmon on the Spawning Grounds

Three behavioral stages were observed in chinook salmon returning to Bogus Creek: migratory, reproductive, and post-reproductive (territorial stage in females). Each stage was characterized by specific behaviors, some of which were restricted to that stage.

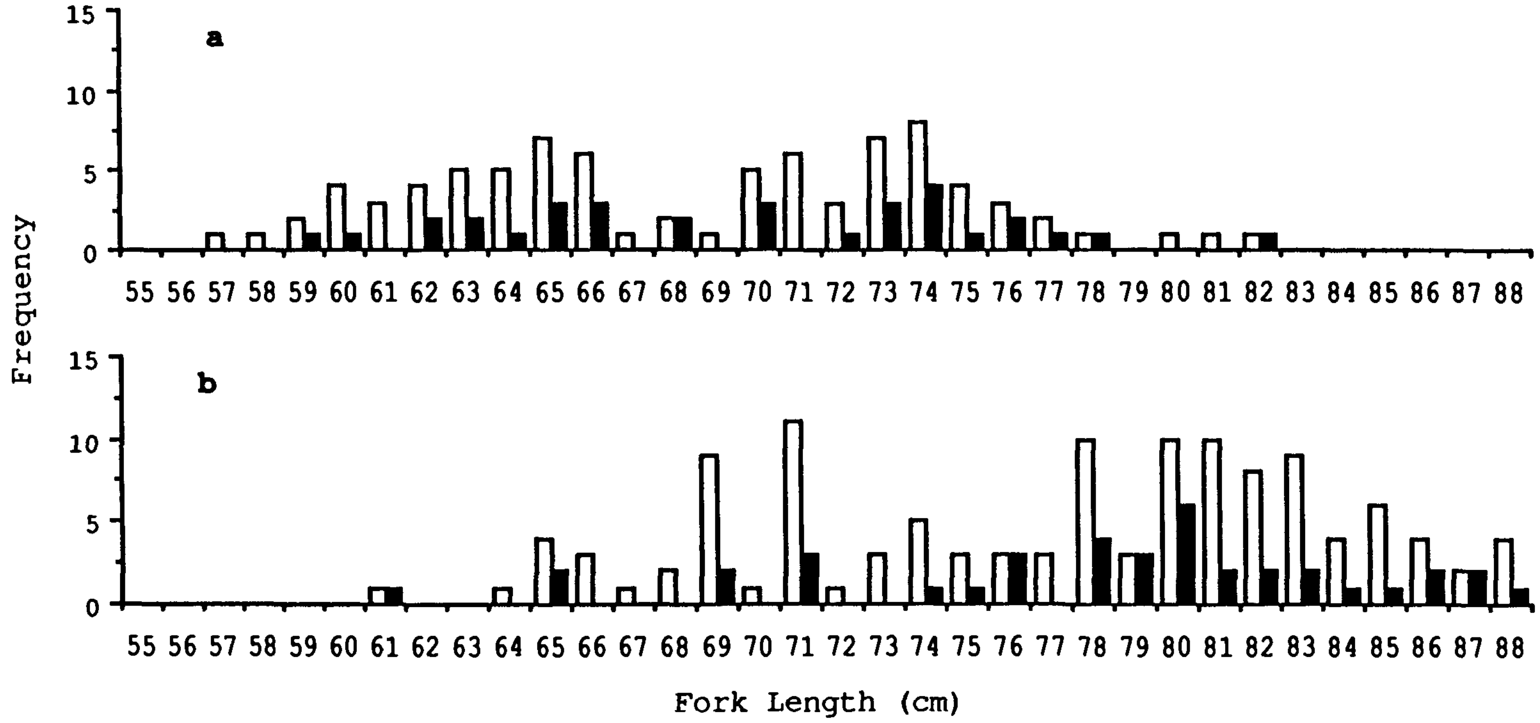


Figure 8. Length Frequency of All Tagged Female Chinook Salmon (White Bars) and of Females Remaining in the Study Area through Spawning and Death (Black Bars) in 1984(a) and 1985(b).

Migratory Stage

The migratory stage was characterized by little physical interaction between individuals. Chinook salmon began entering Bogus Creek in mid-September, migration peaked in the first three weeks of October, and new fish continued to enter through the first week in November. Initially, fish held in pools during the middle of the day, and moved early and late in the day. As the season progressed and the water temperature cooled from highs of 17.8 °C in mid-September to highs of less than 14.5 °C by early October, fish moved throughout the day. Water temperatures from September 22 through October 24 averaged 10.3°C ± 2.6°C and 10.0°C ± 3.7°C for 1984 and 1985, respectively. Fish remained in the deepest water available when not moving upstream.

Reproductive Stage

The reproductive stage for a female began when she initiated excavation of her first nest. This stage ended after approximately three days on her redd. Among females whose history on the spawning gravels was known, all observed spawnings occurred within three days of redd initiation (Table 4). The male reproductive stage began when males exhibited (a) prolonged interest (more than 5 minutes) in a female and (b) courting behavior (i.e. nudge, quiver, move parallel or move side to side, Table 2), or

Table 4. Number of Spawnings That Occurred within Less than One (1), One to Less than Two (2), Two to Less than Three (3), and over Three (>3) Days after the Initiation of Redd Digging among Females of Known Redd Initiation Dates Observed to Spawn in Bogus Creek during 1984 and 1985.

Year	Days after Redd Initiation				Total Number of Spawnings
	1	2	3	>3	
1984	7	2	3	0	12
1985	4	2	2	0	8
Total	11	4	5	0	20

(c) remained in or returned to a satellite position in the face of aggression by a primary male.

Both sexes became reproductive soon after entering the creek if they spawned low in the drainage. In 1984 and 1985, respectively, over 88 percent and 90 percent of the tagged females that spawned in the study area began redd excavation within four days of entering Bogus Creek (Table 5). As a group, males initiated courting in a temporal pattern similar to that of females (Table 5).

Female Reproductive Behavior. The act of digging has been well described for other species of salmonids (Jones and Ball 1954, Sheridan 1960, McCart 1969, Hartman 1970, Tautz and Groot 1975) and was the same for female chinook salmon. In between digs, females rested in or tested (Figure 9) their nests to determine progress.

All females that spawned within the study area and whose activity was followed until they died (n=84, both years combined), dug a single redd. No females were observed to move elsewhere after apparently spawning in their first nest, although 2 of 84 (about 2 percent) were displaced within less than one day on their first nest. Because each of these females was periodically, if not continuously, attacked by adjacent females while starting their first nest, it was unlikely that either spawned before losing their redd site. Each female subsequently

Table 5. Days from Stream Entry until the Initiation of Courting Behavior or The Start of Redd Excavation in Tagged Male and Female Chinook Salmon, Respectively. Based on Fish Observed in Bogus Creek during 1984 and 1985. Percent of Total in Parentheses.

Days after Entry	Number of Males Courting	Number of Females Digging
	1984	
1	5 (35.7%)	12 (48.0%)
2	2 (14.3%)	2 (8.0%)
3	2 (14.3%)	5 (20.0%)
4	1 (7.1%)	3 (12.0%)
5	0 (0.0%)	0 (0.0%)
≥6	4 (28.6%)	3 (12.0%)
	1985	
1	8 (40.0%)	20 (60.6%)
2	5 (25.0%)	7 (21.2%)
3	4 (20.0%)	3 (9.1%)
4	1 (5.0%)	0 (0.0%)
5	1 (5.0%)	1 (3.0%)
≥6	1 (5.0%)	2 (6.1%)

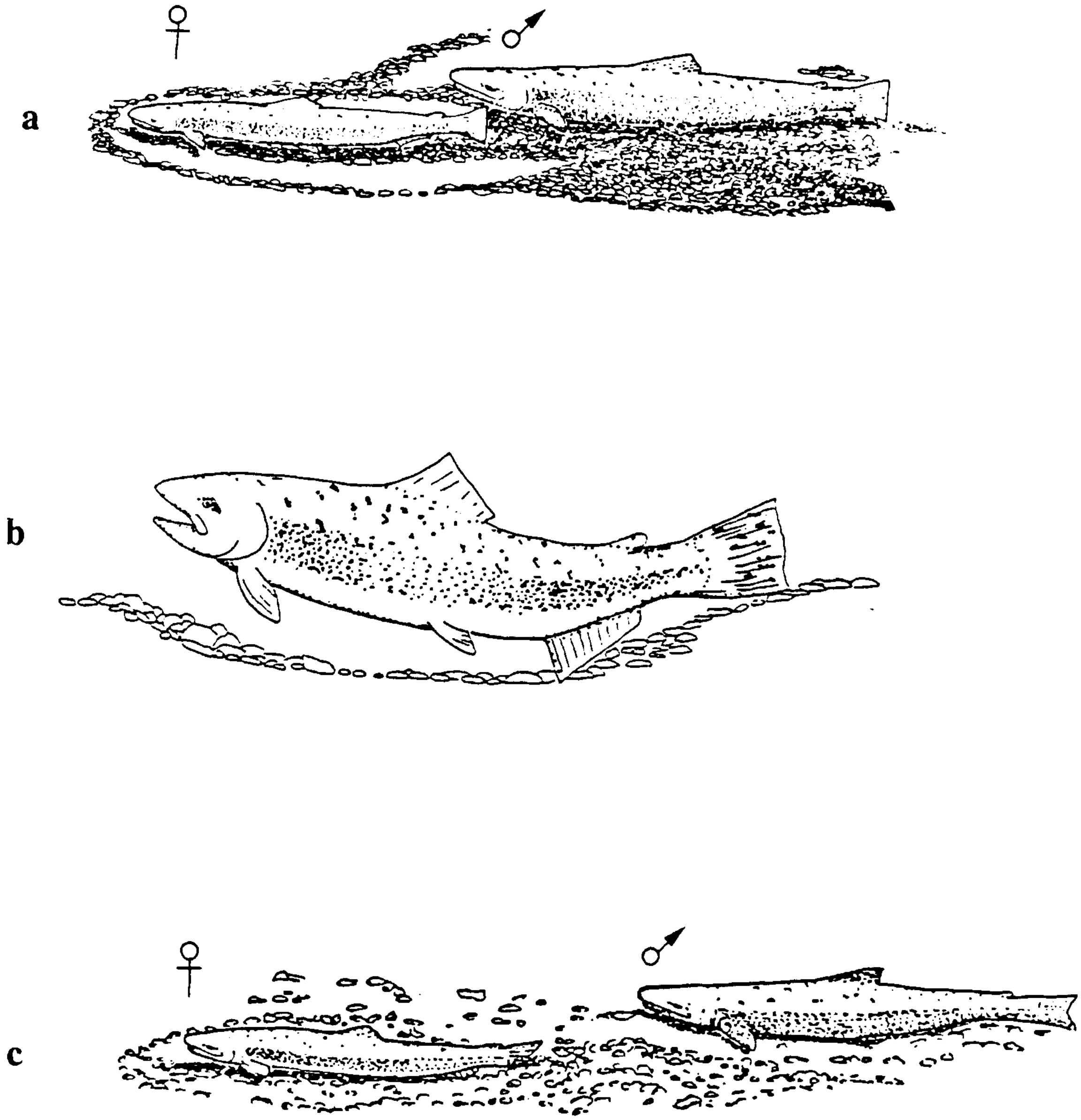


Figure 9. a. Female in Her Nest with Primary Male Downstream and to One Side; b. Lateral View of a Female Testing; c. Top View of a Female Testing with Her Mouth Closed.

established another redd within the study area and remained in or close to the redd until near death.

During the reproductive period, females associated with a succession of males. Some males courted the female, whereas others simply held position next to or near the female. Individual female chinook salmon encountered an average of 5.4 males ± 4.6 males (n=51, 1984 data) during 20 minute focal-female sample periods.

Female courting behavior was not as overt as that of males. Courting behavior involved females nudging males (Figure 10a), moving alongside a male and holding a parallel position close to or touching the male (Figure 10b), or swimming from one side of the male underneath it to the other when both fish were in the nest (Figure 10c). Nudging and move parallel were separate behaviors, both expressed toward primary males when the males were holding away from the nest of a female or returning after chasing another fish. A female also expressed these behaviors toward primary males upon her return to the nest when the male was present. Females crossed under males when both male and female were in the nest.

Females showed aggression toward males by biting, chasing, or pushing them with body or tail. Females expressed these behaviors in the same manner as males. Females were observed to push satellite males downstream

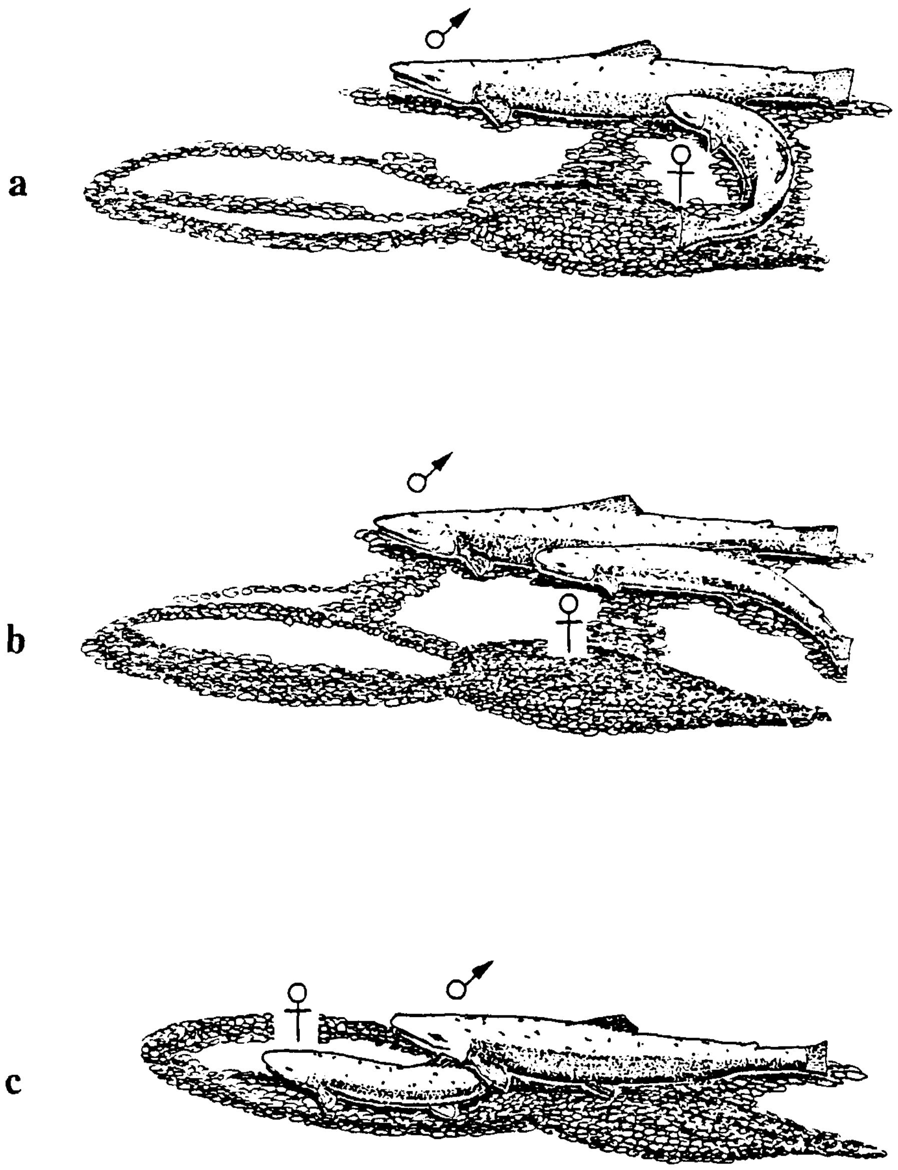


Figure 10. a. Female Nudges Primary Male; b. Female Moves Parallel to the Primary Male; c. Female Crosses Under Primary Male while in Her Nest

out of the redd or the primary male laterally to another position within the redd.

Lone reproductive females exhibited aggressive behavior toward new males initially, regardless of the relative size of the male. At their first encounter a lone female, on her redd, bit or chased intruding males 41 percent of the time (n=200) and there was no difference in the proportion of bite or chase behaviors expressed toward males of different relative sizes (X^2 test). Even primary males which had been with a female more than five minutes faced some female aggression. Ten of 27 females (37 percent) sampled while being courted were observed to bite established, primary males during the 20 minute sample period.

During each of the first three days on their redd, female chinook salmon exhibited statistically significant differences in behavior toward males of different relative sizes (day one: $X^2 = 159.308$, $p < 0.001$, 6 df; day two: $X^2 = 15.251$, $p < 0.025$, 6 df; day three: $X^2 = 36.008$, $p < 0.001$, 6 df, Table 6). During their first day on the redd females exhibited significantly more digs when on a redd with males of the larger size category and fewer when with males of the smaller size category in every comparison (Table 7). Conversely, females were significantly more aggressive toward males in the smaller size category in every comparison and less aggressive

Table 6. Female Behavior toward Males of Different Relative Sizes Exhibited during Her First Three Days on Her Redd (1984 and 1985), and the Number (n) of Different Males of Each Size Group Encountered. Based upon a Summary of 22, 17 and 19 Focal-Female Samples for Days One, Two and Three, Respectively.

			Female Behavior				
Day on Redd	Male Size Relative to Female		Dig	Nudge or Move Parallel	Chase or Bite	No Reaction	Total
One	Smaller	n = 49	9	0	41	52	102
	Equal	n = 41	66	82	27	119	294
	Larger	n = 25	116	51	15	191	373
	Total		191	133	83	362	769
Two	Smaller	n = 34	9	7	25	54	95
	Equal	n = 58	40	34	42	129	245
	Larger	n = 31	7	11	27	38	83
	Total		56	52	94	221	423
Three	Smaller	n = 34	5	3	39	35	82
	Equal	n = 61	32	42	50	119	243
	Larger	n = 15	11	8	7	30	56
	Total		48	53	96	101	381

Table 7. Chi-Square Values for Two by Two Contingency Analyses Comparing Individual Female Behaviors Exhibited toward Males in Two Size Categories. Data Are from Table 5. Significant Differences ($p < 0.05$) in Female Behavior toward Males in Different Size Categories Are Indicated by an Asterisk (*).

		Female Behavior			
Day on Redd	Male Size Categories	Dig	Nudge or Move Parallel	Chase or Bite	No Reaction
One	Smaller vs Equal	9.158*	35.878*	51.207*	3.406
	Equal vs Larger	6.200*	20.820*	7.426*	7.610*
	Smaller vs Larger	20.497*	15.624*	100.788*	0.002
Two	Smaller vs Equal	2.606	2.375	3.640	0.483
	Equal vs Larger	3.146	0.020	8.837*	1.171
	Smaller vs Larger	0.056	1.688	0.827	2.170
Three	Smaller vs Equal	3.039	9.542*	22.451*	0.972
	Equal vs Larger	1.549	0.294	1.924	0.385
	Smaller vs Larger	5.956*	5.123*	18.407*	1.583

toward males of the larger size category (Table 7). Equal sized and larger males received significantly more nudges or move parallels from the female than smaller males, and equal sized males significantly more than larger males (Table 7).

During their second day on the redd the only significant pair-wise comparison indicated that females exhibited significantly more aggressive behavior toward larger males and less toward equal sized males (Table 7). During their third day on the redd, females exhibited significantly more digs, nudges and move parallel behaviors toward equal sized or larger males and less toward smaller males (Table 7). Females exhibited significantly more aggressive behavior toward smaller males and less toward equal sized or larger males (Table 7).

Reproductive females also defended their redd site from intrusion by newly arrived females searching for a redd site and by females on adjacent redds. Female aggression toward neighboring females was expressed by bites (Figure 11). In 44 percent of such attacks (n=61), the territorial females exchanged a rapid series of two or more bites that appeared to involve hard strikes to the side of the opponent, before one or both withdrew. In the other 56 percent of such attacks, only a single bite was observed. Both females returned to their redds within five minutes in 93 percent of all such encounters observed

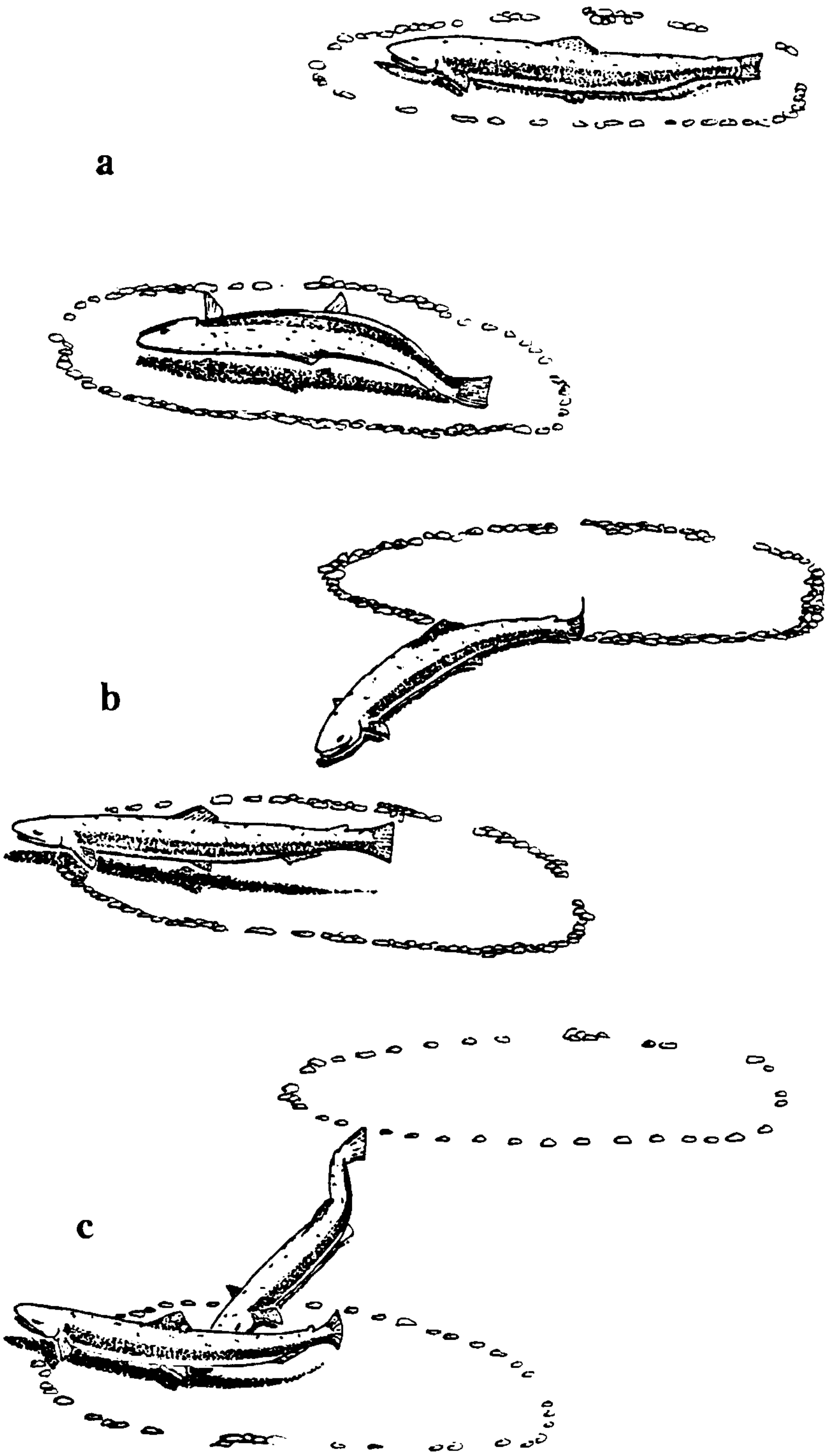


Figure 11. a. One Female in Her Nest while the Other Digs; b. First Female Moves Left to Bite the Other; c. First Female Bites the Other.

(n=61); others may have returned after the samples concluded.

<u>Female Behavior at Spawning</u>. Female behavior just before spawning did not indicate a preference for males of a particular size. Based upon nine focal female samples where female behavior was recorded for 8 to 20 minutes before a spawning, only one aggressive act (a push) was exhibited by a female toward any male during these observations. At least two males were present in each of these observations and smaller males were in the courting groups of 7 of 9 females. Within eight minutes of spawning, female chinook salmon behavior consisted solely of testing their redds and occasionally digging.

The testing posture was identical to that used when spawning, except that the female's mouth may or may not have been open during testing. Females tested at a rate of 0.61 tests ± 0.64 tests per minute (n=9) during the eight minutes prior to spawning. Three of these nine females did not test at all within eight minutes of spawning.

During six behavior samples of females who both tested and spawned while under observation, a total of 63 tests were recorded prior to spawning. During 14 of these tests (22 percent), all males present responded by rushing into the nest alongside the female (i.e. moved parallel). During 10 female tests (16 percent) only the primary male moved parallel to the female, whereas during three other female tests (9 percent) only a single satellite male moved parallel to the female. Satellite males were chased away by the primary male during 10 female tests (16 percent), or did not respond while the primary male nudged or moved side to side over the female during 11 and 15 female tests (17 and 24 percent), respectively.

Of the 27 female tests in which one or more males moved into the nest and parallel to the female, the males involved moved away from the female immediately after moving parallel, moved away after remaining next to the female for two or more seconds, or moved away after one or more males released milt during 63, 18.5 and 18.5 percent of such tests, respectively. The tests during which males released milt were considered false spawnings and each occurred between 5 and 8 minutes prior to the real spawning.

The digging behavior females used to fill their nests was characteristic of all observed spawnings and was used to distinguish an actual spawning from premature male release of gametes (false spawning, Table 2). False spawnings occurred when one or more males moved alongside a testing female and released milt, but the female did not begin filling her nest afterward.

At the time of spawning the female moved into the nest and held a posture identical to testing, with her tail on the bottom, her body arched extending her anal fin into the gravel, and her mouth open (Figure 12a). The primary male immediately moved parallel to the female and into a similar posture (Figure 12b), sometimes tilting to the side to position his vent closer to that of the female. Satellite males rushed into the nest in some, but not all spawnings when such males were present (Figures 12c and 12d). In 3 of 35 observed spawnings the female moved parallel to the primary male, already in the nest, and began spawning.

Female digging rate and orientation within the nest differed between pre- and postspawning. Prior to spawning, the female concentrated most of her digging through the deepest portion of her nest and dug with her body parallel to stream flow. The last excavational digs occurred at a rate of 0.5 digs per min ± 0.2 digs per min ($n = 8$) during the five minutes prior to spawning. Once the female spawned, she immediately began to fill in her nest. She moved to the upstream edge of the depression to one side of the center axis, faced at an angle to the current and dug into the upper edge of the nest. This was repeated almost immediately on the opposite side of the upstream edge of the nest and continued with the female alternating sides until the eggs were covered with gravel.

The digging rate which females used to cover their nests varied from 4 to 10 digs (each dig consisted of a

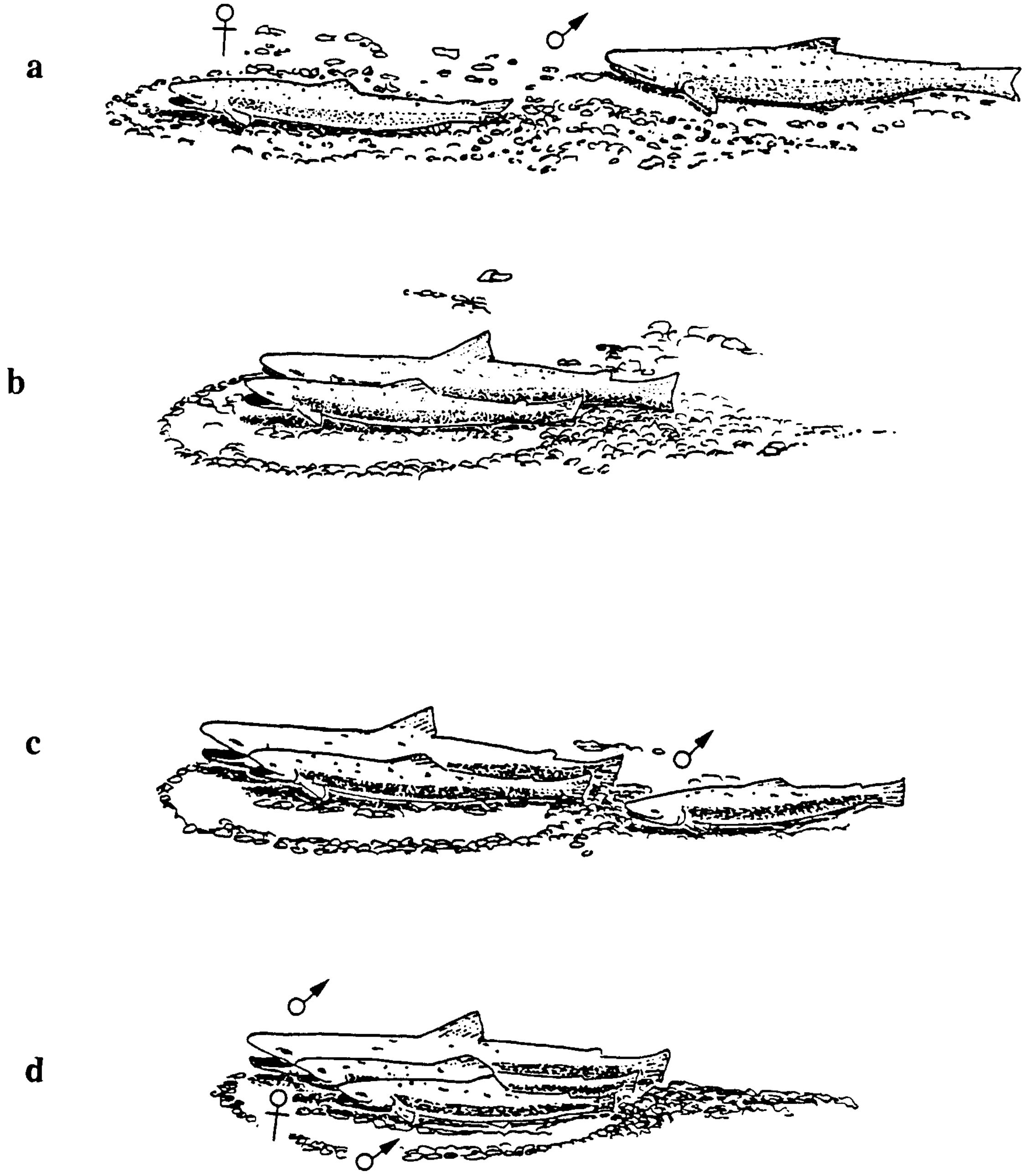


Figure 12. a. Female Tests in Her Nest while Primary Male Holds Downstream; b. Primary Male Moves Parallel to the Female in Her Nest; c. The Female and Primary Male Begin to Spawn while a Satellite Male Moves up from Downstream; d. The Satellite Male Moves Parallel to the Female and Begins to Spawn.

series of flexures) per minute for the first minute and within several minutes tapered off to 1 to 3 digs per minute. The average digging rates for minutes one through five postspawning were: 5.6 ± 1.8, 4.7 ± 1.4, 3.1 ± 0.9, 2.7 ± 1.3, and 2.6 digs/min ± 0.8 digs/min (n = 7), respectively. In contrast, an average digging rate of 0.51 digs/min ± 0.28 digs/min (n = 22) was calculated for females during their first day on the redd from behavior samples in which no spawning occurred. This was similar to the digging rate calculated for females immediately prior to spawning.

Multiple spawnings for the same female were recorded at 7 hours 49 minutes apart for one female chinook salmon, and 18 hours 16 minutes apart for another. In the first case, repeated observations of the female between spawnings indicated that the spawnings were consecutive. In the second case, the spawnings were on successive days. Presumably, an unobserved spawning occurred between observed spawnings in the second case. Based on these data it took approximately nine hours for this second female to prepare second and third nests, if each took approximately the same time to construct.

Based upon observations of known spawnings and on records of female "filling behavior" and digging rates, time of spawning was established for 18 spawnings in 1984 and 21 in 1985. Spawning times were approximately evenly distributed throughout daylight hours (Table 8).

Male Reproductive Behavior. Four of 36 tagged males in 1985 (all over 80 cm FL) were observed to go through a short, 1 to 2 day, prereproductive phase. This phase was characterized by males exhibiting T-displays toward females and other males, but no courting behavior toward females. During this phase, pairs of males were observed to go through sequences of displays and charge-bites that lasted over an hour (Table 2). These sequences were not expressed in conjunction with a male defending a female, although similar behaviors were observed between reproductive males.

Male chinook salmon used a number of behaviors when courting reproductive females. Males initiated courting behaviors from a "holding position" located almost behind and to one side of the female (Figure 13a).

Nudging was the simplest male courting behavior. From a holding position, the male moved forward and nudged the female near her anal fin (Figure 13b). The nudge and quiver was an elaboration of the nudge consisting of the nudge followed by the male erecting his dorsal fin and producing high frequency, low amplitude, lateral undulations with his body while remaining alongside the female (Figure 13c); males appeared to vibrate.

Table 8. Distribution of Spawnings by Hourly Intervals over Time (24 Hr Scale) for Spawnings Observed (37) and Inferred (2) from Female Behavior during 1984 and 1985.

	Hour of Day											
Year	8	9	10	11	12	13	14	15	16	17	18	Total
1984	0	2	3	5	2	1	2	0	0	2	1	18
1985	2	1	0	2	2	4	2	0	4	4	0	21

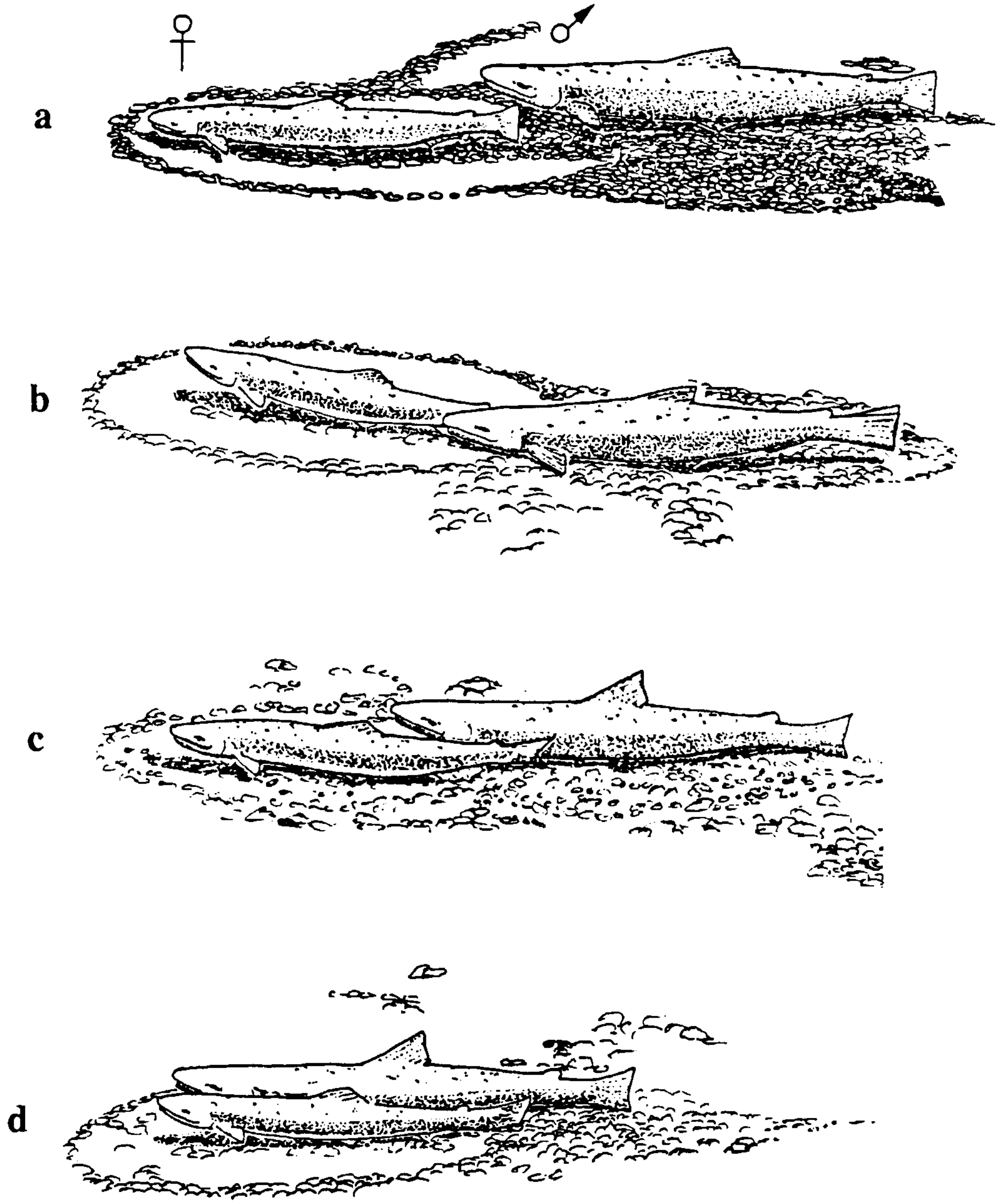


Figure 13. a. Primary Male Holds just Downstream and to One Side of the Female; b. Primary Male Moves up and Nudges the Female; c. Primary Male Quivers alongside the Female; d. Primary Male Moves Parallel to the Female.

Courting males also moved up from the holding position to a position head-to-head and parallel with the female (i.e. move parallel, Figure 13d). This was a rapid movement and was also used by males entering the nest to spawn. One or more of the males in attendance moved parallel to the female when she tested during 43 percent of the 63 female tests used in this analysis (see Female Behavior at Spawning). On two occasions when females temporarily left the nest, primary males who remained stationary touching the bottom of the nest were courted (move parallel and nudge) briefly by a satellite male.

Males used the move side-to-side behavior (Figure 14a) when they courted a female and to position themselves between a female and intruding males. Once a side-to-side movement was completed, a male could T-display to (Figure 14b) or push (Figure 14c) other males that had encroached on the redd. Males also defended females by biting or chasing-off intruding males (Figure 15a and 15b). Smaller males comprised 78 percent of the males (n=74) nudged, pushed, chased or bit by primary males.

Reproductive males swam around over spawning gravels until they located a reproductive female approaching the time of spawning. Male behavior at this point depended upon a number of factors: 1) the response of the female to his presence, 2) whether other males were courting the

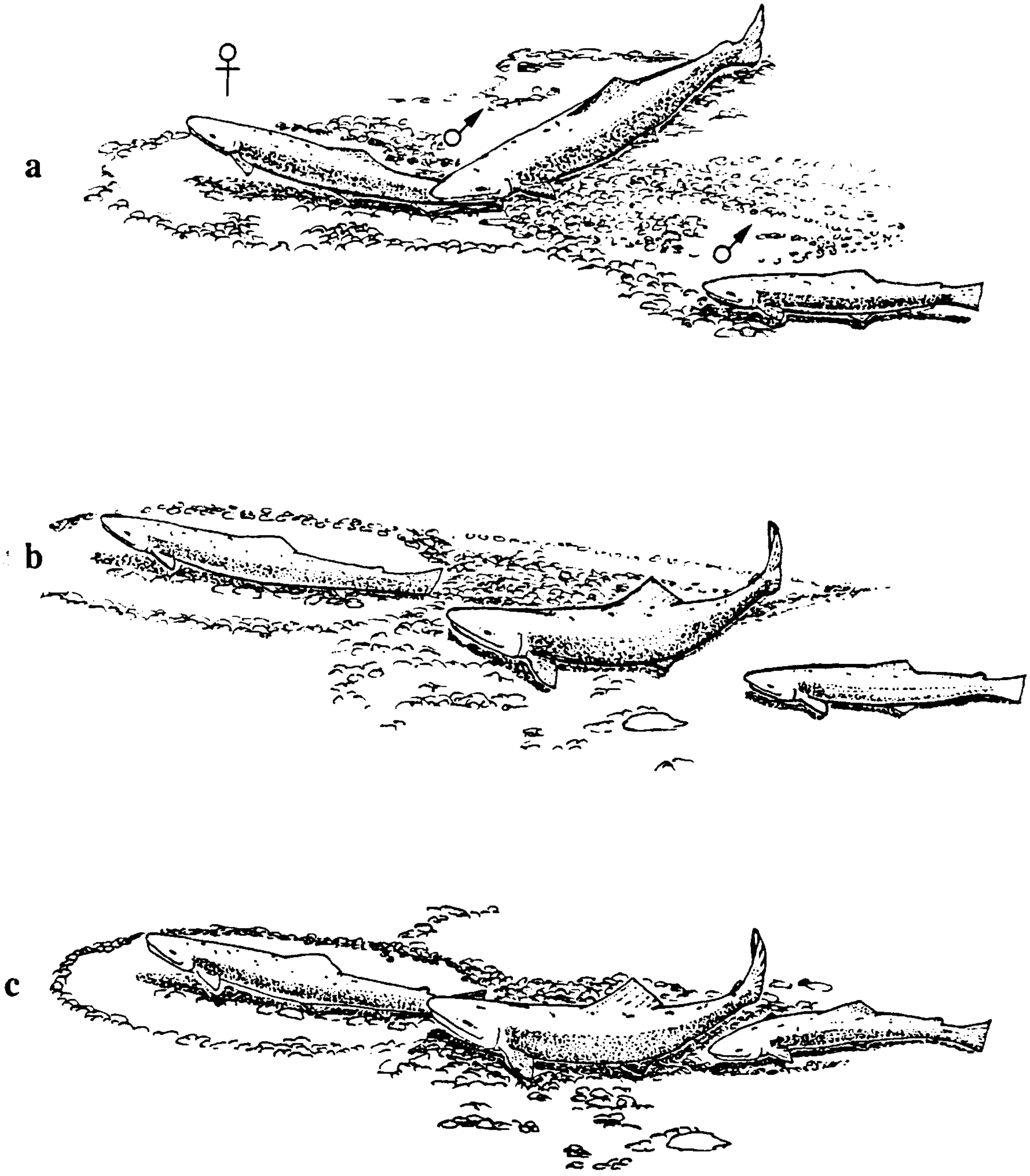


Figure 14. a. Primary Male Moves Side to Side over the Tail of the Testing Female while a Satellite Remains Downstream; b. Primary Male T-Displays to the Satellite Downstream; c. Primary Male Pushes the Satellite Male Downstream while Displaying.

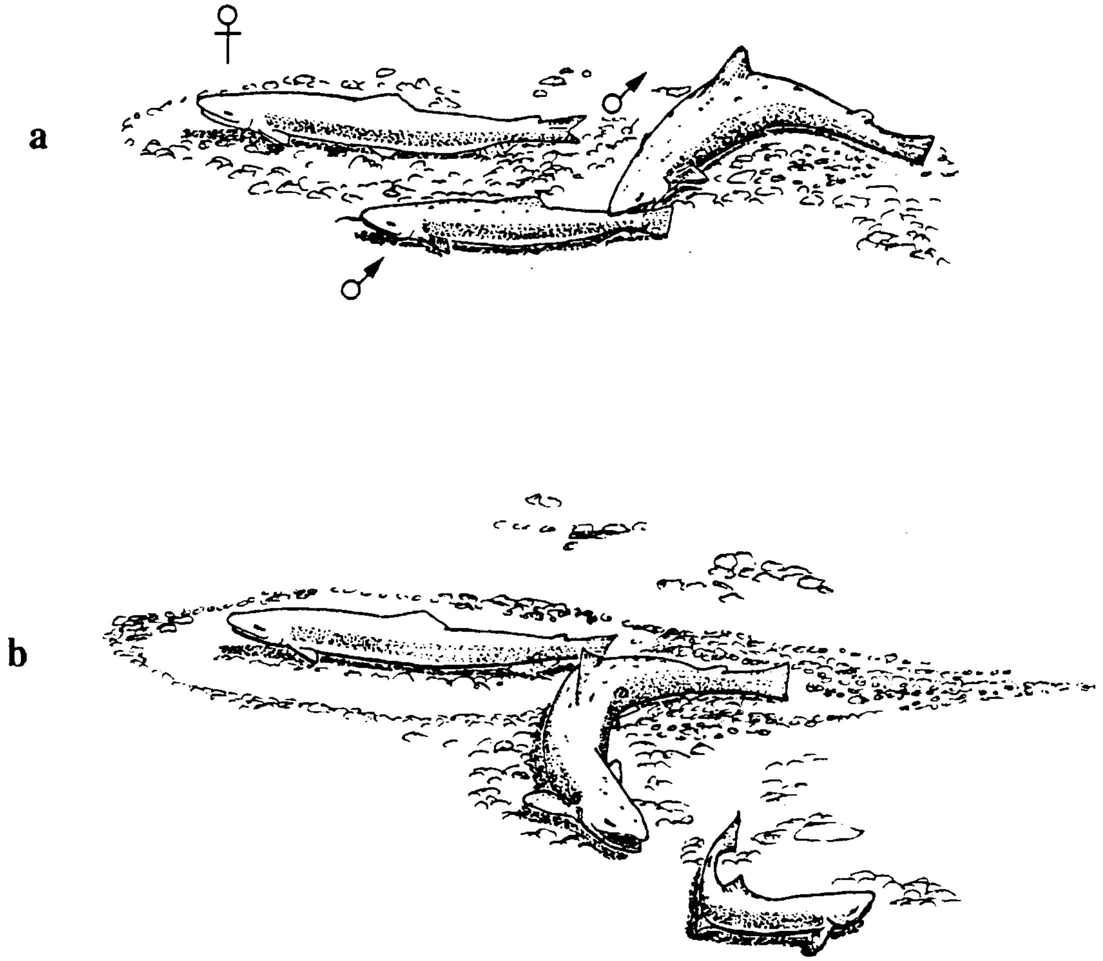


Figure 15. a. Primary Male Bites a Satellite Male on the Caudal Peduncle; b. Primary Male Chases the Satellite Male Downstream away from the Female.

female, and 3) the relative size of any other male(s) present.

When a male located a lone, reproductive female on her nest, his most frequently observed behavior was to simply move onto the redd and hold position (102 of 233 encounters, 44 percent). In about 65 percent of these encounters (n=102) males left the redd without exhibiting another behavior; in another 22 percent, males attempted to court the female after holding briefly (data for 13 percent of these 102 encounters not presented). Males courted (nudge, nudge and quiver, move parallel and move side to side) lone females as a first behavior in about 25 percent of the encounters and swam through the redd without stopping in another 25 percent (n = 233). Males also T-displayed to (4 percent), pushed (1 percent) or bit (1 percent) lone reproductive females as a first behavior (n = 233).

When a wandering male first encountered a courting pair (n=64), his initial behavior was to either move through the redd and away (22 percent), move onto the redd and hold (48 percent), court the female (19 percent) or T-display just upstream of the redd (11 percent of such encounters). Whether the female was alone or not, initially, new males usually moved near a female and reacted to her behavior rather than directing a behavior toward her.

When associated with females, males responded differently to other males of different relative size (X^2 = 129.984, $p < 0.001$, 8 df, Table 9). Males swam away or drifted downstream significantly more frequently when confronted by a larger male, and less frequently than expected when confronted by equal sized or smaller males (Table 10).

Males T-displayed significantly more frequently than expected when confronted by equal sized males and less frequently when confronted by either smaller males or larger males (Table 10). Males nudged or pushed equal sized or smaller males significantly more frequently than larger males (Table 10). There were significant differences in the relative frequencies of chase/bite responses in every comparison. Larger males were always chased or bit less frequently and smaller males more frequently than expected (Table 10).

When more than two males located a female prior to spawning (n=11), the males appeared to establish hierarchies with satellite males arranged linearly (Figure 16a), in a crescent shape (Figure 16b), or linearly with a peripheral satellite (Figure 16c) in 5, 5 and 1 observations respectively. The primary male attempted to drive other males away from the redd, while satellite males attempted to get close to the female and court her. Satellite males directed courting behavior toward the

Table 9. Male Behaviors Directed toward Males of Different Relative Sizes. Based upon a Summary of 12 Focal-Male Samples Taken When Tagged Males Were Associated with a Female while in Primary or Satellite Status during 1985. (n = Number of Males Encountered).

Opponent Size Relative to Tagged Male		Tagged Male Behavior					
		Swim Away or Drift Down	No Reaction	T-Display	Nudge or Push	Chase or Bite	Total
Smaller	n = 28	1	18	15	25	49	108
Equal	n = 23	5	15	27	28	26	101
Larger	n = 18	24	6	4	2	1	37
Total		30	39	46	55	76	246

Table 10. Chi-Square Values for Two By Two Contingency Analyses Comparing Individual Male Behaviors Exhibited toward Males in Two Size Categories. Data Are from Table 8. Significant Differences ($p < 0.05$) in Male Behavior toward Males in Different Size Categories Are Indicated by an Asterisk (*). Not Valid Indicates Inadequate Frequencies for Valid Comparison.

Male Size Categories Compared	Tagged Male Behavior				
	Swim Away or Drift Down	No Reaction	T-Display	Nudge or Push	Chase or Bite
Smaller vs Equal	Not Valid	0.129	5.362*	0.577	8.739*
Equal vs Larger	58.565*	0.039	3.941*	7.928*	9.134*
Smaller vs Larger	78.959*	0.001	0.229	5.725*	22.207*

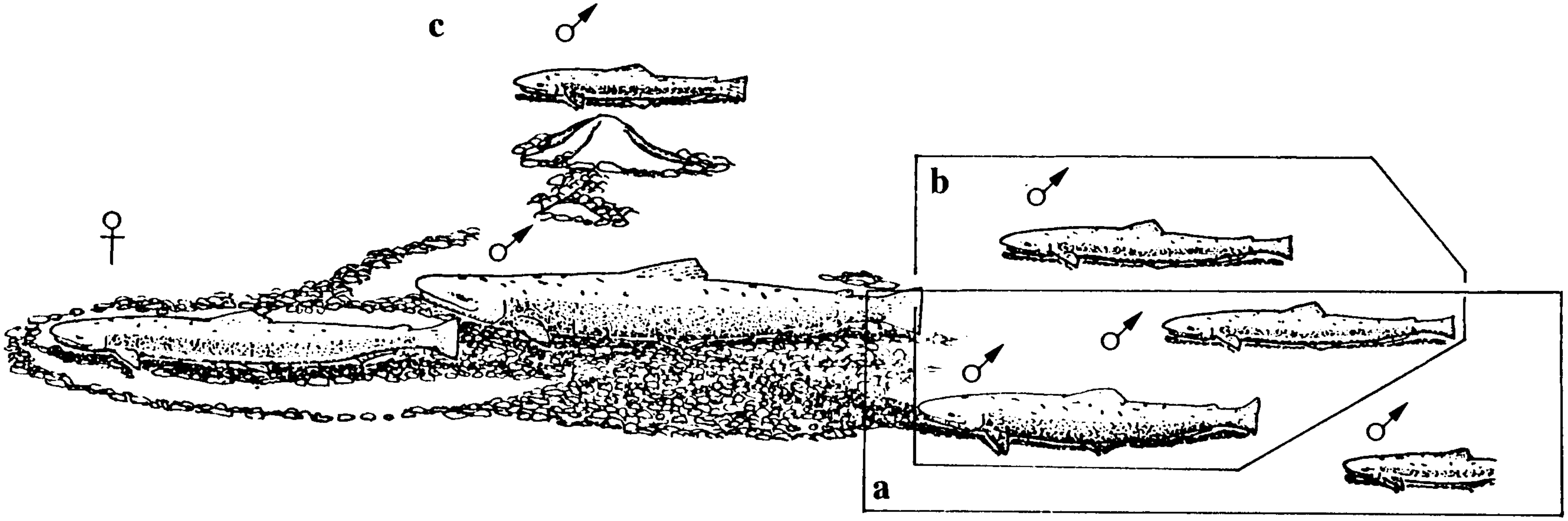


Figure 16. a. Linear Hierarchy of Males Downstream of a Female (inside Rectangle); b. Crescent Shaped Hierarchy of Males (inside Polygon); c. Location of a Peripheral Satellite Male behind a Rock in Relation to the Primary Male and Female.

female when the primary male was away from the redd. In one case, when the primary male was scared off by the observer, a satellite jack moved in, courted the female for about two minutes, and then fertilized a large spawning of eggs by himself.

Unlike females that stayed within a limited geographic area once they became reproductive, males tended to roam. In 1985, 27 tagged males were observed exhibiting some reproductive behavior while within the study area; of these males, 17 were observed from the onset of courting behavior through death. For these 17 males, reproductive lifetimes averaged 8.9 days ± 2.7 days (n=17). Male fork length was not significantly correlated with reproductive lifetime ($r_s = 0.181$, $0.20 < p < 0.50$). The average male lifetime on the spawning grounds, from initiation of the reproductive stage until death, was 10.2 days ± 2.6 days (n=17). The small sample size for males precluded comparison of possible differences in reproductive lifetimes between early and late spawners.

Male Behavior at Spawning. As spawning approached, male courtship involved body contact with the female using nudge, nudge and quiver, move parallel or move side to side behaviors. Courting males averaged 4.2 courting behaviors ± 2.4 courting behaviors per min (n=8) directed toward the female during the eight minutes prior to spawning. As spawning approached, additional males were attracted to the group. Primary male aggressive behavior temporarily repelled satellite males from the vicinity of the nest.

A total of 35 undisturbed spawnings were observed during 1984 and 1985. The number of males associated with a female at the time of spawning varied from 1 to 7, with two-male spawnings observed on 18 occasions (Table 11). Twenty-nine of 35 spawnings involved more than one male. Primary males always spawned and they entered the nest first (79 percent) or at the same time (14 percent) as the first satellite in 27 (93 percent) of these 29 spawnings (Table 11). One or more satellite male(s) did not spawn in 11 of 29 (38 percent) multiple-male spawnings. In general, the more males present the less likely all were able to spawn (Table 11).

In 21 of 29 spawnings (72 percent) involving more than one male, male order of entry into the nest and position in relation to the female and primary male were recorded. Lone satellite males did not enter the nest in three spawnings (14 percent, n=21). In two spawnings (9.5 percent) the primary male entered the nest after the first satellite male (i.e. satellite male closest to the pair just prior to spawning) and on the opposite side of the female. In the remaining 16 spawnings, the first satellite male entered the nest after the primary male and either spawned alongside the female (12, 57 percent), alongside

Table 11. Number of Males Involved in Courting Groups and Their "Success" in Entering the Nest of a Female at the Time of Spawning. These Data Were Based on Undisturbed Chinook Salmon Spawnings Observed in Bogus Creek during 1984 and 1985. Number of Obs. Refers to the Number of Observations Falling into a Category (e.g., Number of Observations in which All Males Spawned Was 24 of 35).

	Number of Males in Courting Group						
Number of Obs.	1	2	3	4	5	7	Total Freq.
Frequency Observed:	6	18	2	6	2	1	35
Proportion of Spawnings in which All Males Spawned:	1.00	0.78	0.50	0.50	0.00	0.00	24
Proportion of Spawnings Involving Two or More Males in which the Primary Male Entered Nest First:	-	0.83[a]	1.00	0.83[b]	0.50	0.00	23
Proportion of Spawnings Involving Two or More Males in which the Primary Male Entered Nest at Same Time As Satellite:	-	0.06	0.00	0.17	0.50	1.00	4
Proportion of Spawnings Involving Two or More Males in which The Primary Male Entered Nest Second:	-	0.11	0.00	0.00	0.00	0.00	2

[a] Two spawning records were unclear regarding rank order of entry into nest, therefore it was assumed that the primary male entered first since it was not recorded otherwise.

[b] One spawning record was unclear regarding rank order of entry into nest, therefore it was assumed that the primary male entered first since it was not recorded otherwise.

the primary male (2, 9.5 percent) or in between the female and primary male (2, 9.5 percent).

Tertiary and quaternary spawning males moved in between the female and primary male upon entering the nest in 3 of 11 spawnings involving more than two males. This tactic resulted in late spawning males being in close proximity to any unfertilized eggs left in the nest when they released their milt.

In all observed spawnings, primary males were at least as large (43 percent) or larger than the females with whom they spawned (n=35, Table 12). In three cases, primary males, after they had released milt, attempted to drive one or more satellite males from the nest. All of these satellite males were successful in entering the nest and none were driven away before they had time to release milt. All males involved in a spawning remained in the nest for about one minute postspawning, while the female began covering her eggs.

In 10 spawning observations where male behavior was noted for at least 10 minutes postspawning, primary males left the nest area within five minutes postspawning in four of these cases. All satellite males that appeared to spawn remained with the female as she filled her nest, even after the primary male left.

Male-male competition for access to reproductive females increased in the latter half of both 1984 and 1985

Table 12. Relative Size of Primary Males As Compared to Females of Known or Estimated Size Involved in Spawnings Observed on Bogus Creek during 1984 and 1985. The Number of Observations Involving Fish of Known Size Are Indicated below Female Size Known, Male Size Known, or Both Know. Otherwise Fish Size Was Visually Estimated.

Year	Female Size Interval (cm)	Relative Size of Primary Male			Female Size Known	Male Size Known	Both Known
		Smaller	Equal	Larger			
1984	60.0 - <69.9	0	4	3	2	0	0
	70.0 - <79.9	0	4	7	2	0	0
	80.0 - <89.9	0	1	0	0	0	0
1985	60.0 - <69.9	0	1	2	0	1	1
	70.0 - <79.9	0	3	3	3	0	1
	80.0 - <89.9	0	2	3	2	2	0
	No Size Recorded	0	0	2	0	1	0
Total		0	15	20	9	4	2

spawning seasons based upon the number of males associated with a female just prior to spawning. However, the difference in the number of males associated with prespawning females during the first and second halves of each season was only significant during 1984 (1984 - $U_{8,11} = 75.5$, $p < 0.01$; 1985 - $U_{6,10} = 40$, $0.20 < p < 0.50$). In 1984, an average of 1.9 males ± 1.1 males (n=11) were associated with females observed to spawn prior to 10 October (the mid-point of the spawning run); after that date an average of 4.0 males ± 1.6 males (n=8) were associated with females observed to spawn. In 1985, an average of 2.0 males ± 1.1 males (n=6) were associated with females that spawned prior to 8 October; after that date, an average of 2.4 males ± 0.7 males (n=10) were associated with females observed to spawn.

Success of Individual Males. In 1985, tagged males larger than 80 cm were observed in primary status proportionally more often than those smaller than 80 cm, whereas the reverse was true for satellite status (Figure 17). For males in excess of 80 cm fork length, an average of 44 percent ± 19 percent of observations were of primary status, whereas for males less than 80 cm fork length an average 8 percent ± 9 percent of observations were of primary status. Proportions of observations in which males were in a subordinate status averaged 27 percent ± 11 percent for males

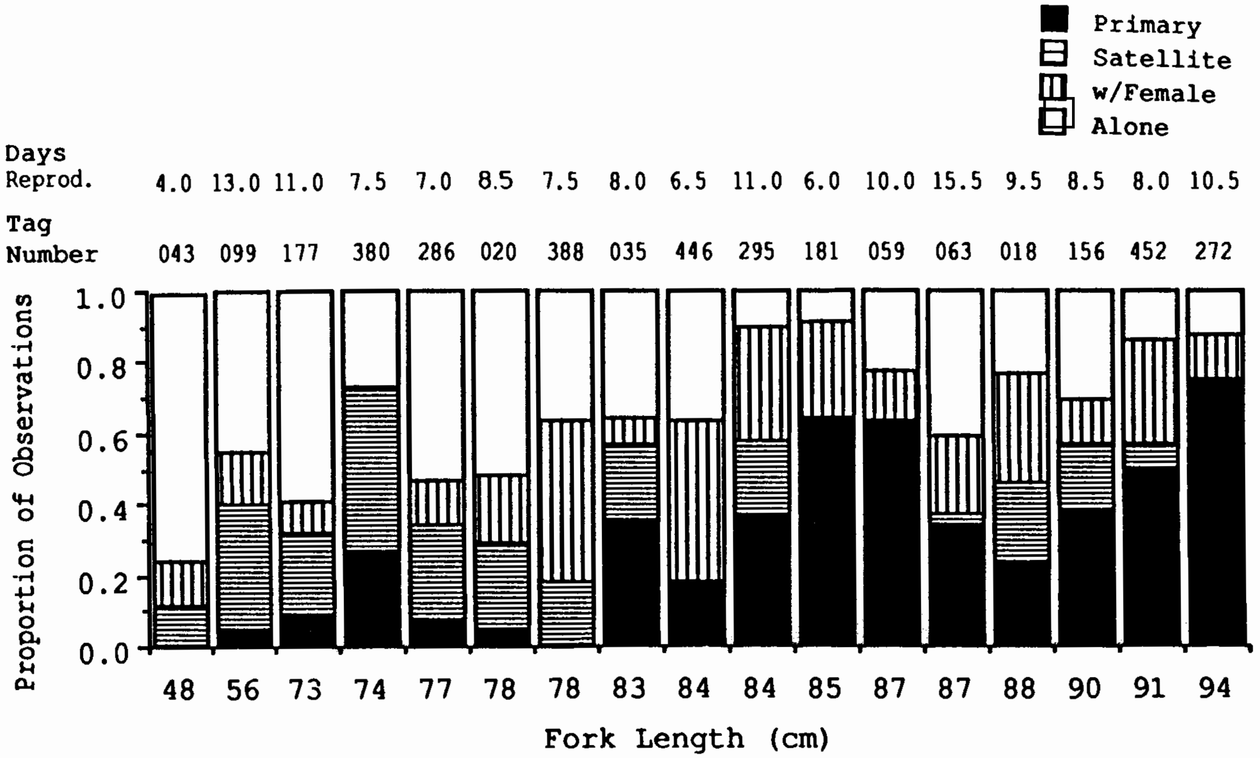


Figure 17. The Proportion of Observations in which Each Tagged Male Was a Primary, a Satellite, with a Female (Non-courting), and Holding Alone or Wandering Arranged in Order of Increasing Male Fork Length. Tag Number and Number of Days Reproductive Are Presented for Each Male (1985 Data).

less than 80 cm, whereas males larger than 80 cm were rarely observed in a subordinate status (average 9 percent ± 10 percent).

In 1984, male number 2 and male number 3 became reproductive early in the season and were observed to participate in four spawnings with three different females and three spawnings with two different females, respectively (Table 13). Four spawnings were the most observed for a single male during either year. Similarly, in 1985, tagged male 059 became reproductive early in the season and during his 10 day reproductive lifetime male 059 was observed to spawn one time each with three different females (Table 13). Male 059 was in primary male status during 64 percent of his observations (Figure 17). Male 059 interacted with two other larger than average-sized tagged males; both 035 and 063 were subordinate to him and remained so throughout his life.

Male 063 had the longest reproductive lifetime of any tagged male in the study area, 15.5 days (Figure 17). He was a primary male in 34 percent of his observations (Figure 17), but was never observed to spawn.

Male 035 was a satellite to 059 on two occasions when no spawning was observed, and to an 84 cm tagged male on another occasion. Males 059 and 035 swam in the same area of spawning gravel. Male 035 was only observed in primary status after 059 began to loose strength about two

Table 13. Number of Spawnings Observed, Spawning Date, Days Reproductive, Fork Length (FL) in cm, and Hierarchy Status prior to Spawning of Recognisable Male Chinook Salmon during 1984 and 1985. Total Number of Males and Fork Length of the Female Involved in Each Spawning Are Included. Non-Tagged Males Are Signified by One Digit Numbers and Tagged Males by Three Digit Numbers. Days Reprod. Is the Number of Days after the Start of Courting for the Male That the Spawning Took Place. Estimated Lengths Are Indicated by "≈". Pri Denotes Primary Male Status at the Time of Spawning; Sat Denotes Satellite Status.

Male #	Spawning Date	Days Reproductive	Male FL	Status	Total Number of Males Involved	Female FL
2	28 Sep.	?	66	Pri	2	66
2	2 Oct.	?	66	Sat	2	≈78
2	2 Oct.	?	66	Sat	2	≈73
2	2 Oct.	?	66	Sat	5	≈78
3	2 Oct.	?	≈80	Pri	2	≈78
3	2 Oct.	?	≈80	Pri	2	≈73
3	2 Oct.	?	≈80	Pri	5	≈78
106	3 Oct.	?	85	Pri	1	≈75
452	30 Sep.	3	91	Pri	2	82
059	4 Oct.	2	87	Pri	2	?
059	4 Oct.	2	87	Pri	1	81
059	10 Oct.	8	87	Pri	4	76
020	4 Oct.	1	78	Sat	4	≈83
099	10 Oct.	5	56	Sat	2	76
272	12 Oct.	2	94	Pri	3	65
272	19 Oct.	9	94	Pri	2	?
035	13 Oct.	6	83	Pri	2	≈83
295	17 Oct.	6	84	Sat	2	≈84
295	18 Oct.	7	84	Pri	2	≈63

days before death. Male 035 was a primary male during his one observed spawning (Table 13), which occurred the day male 059 died.

Male 272, the largest tagged male observed (94 cm), became reproductive during the peak of spawning, 10 October 1985. He was never observed in satellite status, had the highest proportion of observations in primary status of any tagged male (75 percent, Figure 17), and was observed to spawn as a primary on two occasions (Table 13).

Male 295 also became reproductive during the peak of spawning (12 October) and was the only tagged male observed to loose primary status just before spawning and spawn as a satellite (Table 13). The new primary male was approximately the same size as male 295, and took over without any aggressive behavior two minutes before spawning occurred. Nonetheless, male 295 was of primary status in about 37 percent of his observations (Figure 17) and spawned as such in his other observed spawning (Table 13).

Two tagged males were observed to spawn as satellites: males 020 and 099 (Table 13). Each of these males entered the nest at spawning after the primary male (020 was the second satellite male to enter the nest) and each moved in between the primary male and the female from a downstream position.

Although the mean estimated number of spawnings was higher for tagged males larger than 80 cm (7.1 spawnings ±

4.1 spawnings, n=10) than for those less than 80 cm (4.1 spawnings ± 3.1 spawnings, n=7), the difference was not significant ($U_{7,10} = 50$, $0.10 < p < 0.20$, Table 14). The estimated number of spawnings for a single male ranged from 1 to 12. Males in predominantly satellite status were estimated to be involved in up to eight spawnings, whereas three different primary males spawned an estimated 12 times each (Table 14). Although male 063 was not observed as a primary proportionally as often as males 059 or 272, he was, nonetheless, estimated to spawn the same number of times as the later two males (Figure 17, Table 14). The number of estimated spawnings for males 063 and 099 can in part be attributed to their longevity on the spawning grounds (Figure 17, Table 14).

Male reproductive behavior often lasted until males were almost dead. Six of 17 (35 percent) tagged males (all over 80 cm) were observed courting females to within one day of death, and another 29 percent courted females to within two days of death. All males eventually weakened and started moving slowly downstream both passively and actively.

Female Postreproductive Stage

After spawning, most female chinook salmon actively defended their redds ("territorial" behavior) until they were close to death. In 1984 and 1985, 29 of 38 females

Table 14. Observed and Estimated Number of Spawnings (Spw.) Per Tagged Male Chinook Salmon during 1985. Male # Is the Male's Tag Number. All Lengths Measured as Fork Length (FL) in cm. Pri Denotes Primary Male Status at the Time of Spawning and Sat Denotes Satellite Status. Pri/Sat Denotes a Male That (Probably) Spawned as a Primary and a Satellite in Separate Spawnings, but Was More Often Primary. The Reverse Is True for Sat/Pri.

Male #	Male FL	Status	Obs. Spw.	Est. Spw.	Total Spw.
272	94	Pri	2	10	12
452	91	Pri/Sat	1	5	6
156	90	Pri/Sat	0	7	7
018	88	Pri/Sat	0	3	3
059	87	Pri	3	9	12
063	87	Pri	0	12	12
181	85	Pri	0	6	6
446	84	Pri	0	1	1
295	84	Pri/Sat	2	7	9
035	83	Pri/Sat	1	2	3
020	78	Sat	1	2	3
388	78	Sat	0	2	2
286	77	Sat	0	1	1
380	74	Sat/Pri	0	8	8
177	73	Sat/Pri	0	6	6
099	56	Sat/Pri	1	7	8
043	48	Sat	0	1	1

(76 percent) and 38 of 46 females (83 percent), respectively, were observed behaviorally protecting their redds by chasing or biting intruding fish. Twelve of 29 (41 percent) and 13 of 38 (34 percent) of the territorial females, in 1984 and 1985 respectively, actively defended their redds to within one day of death. The average number of days territorial (start of redd excavation to last observed redd defence) for these females was 6.4 days ± 2.2 days (n=29) and 7.3 days ± 2.6 days (n=38) for 1984 and 1985 respectively.

Nine of 38 (24 percent) and 8 of 46 (17 percent) female chinook observed throughout their time on the spawning ground in 1984 and 1985, respectively, were never observed to exhibit territorial behavior. Despite such lack of overt territorial behavior, other females did not re-excavate their redds while these females occupied them. Thus, the presence of a female kept other females from re-excavating a redd, even when territorial behavior was not expressed. Moreover, since female fork length was not correlated with number of days on the redd in 1984 (r_S = 0.260, n=28) or in 1985 (r_S = 0.169, n=41), female size did not affect her ability to protect her redd.

After starting a redd a female remained within the nest, just below the tailings or in a nearby pool until she was no longer able to resist the current. In 1984 and 1985, females spent an average of 7.6 days ± 2.3 days (n=38) and 8.8 days ± 2.5 days (n=46), respectively, on their redds before death. Measurement errors in the raw data used to calculate these averages were less than one day in 1984 and less than 0.5 day in 1985.

Carcass Recoveries

In 1984, very few (13) jack carcasses were recovered relative to adult males (124) or females (409), and the peak recovery of jack carcasses came just after those of adult males and females (Figure 18a). In 1985, there was a distinct difference in the recovery dates of jack carcasses and those of adult males and females; jack carcasses were recovered later in the season than either adult males or females (Figure 18b).

In 1985, when the tagging weir retained all dead and morbid spawners, the jack to adult male carcass ratio for the study area was 1:1.93 (130:251), whereas the jack to adult male ratio among live fish passing the counting weir was 1:1.07 (1132:1214). These frequencies were significantly different ($X^2 = 25.763$, $p \leq 0.001$, 1 d.f.) indicating that jacks moved above the counting weir in a greater proportion than adult males.

There was a significant difference in the number of jack, adult male and female carcasses recovered on the tagging weir as compared to upstream in the study area in 1985 ($X^2 = 27.463$, $p < 0.001$, 2 d.f.; Table 15).

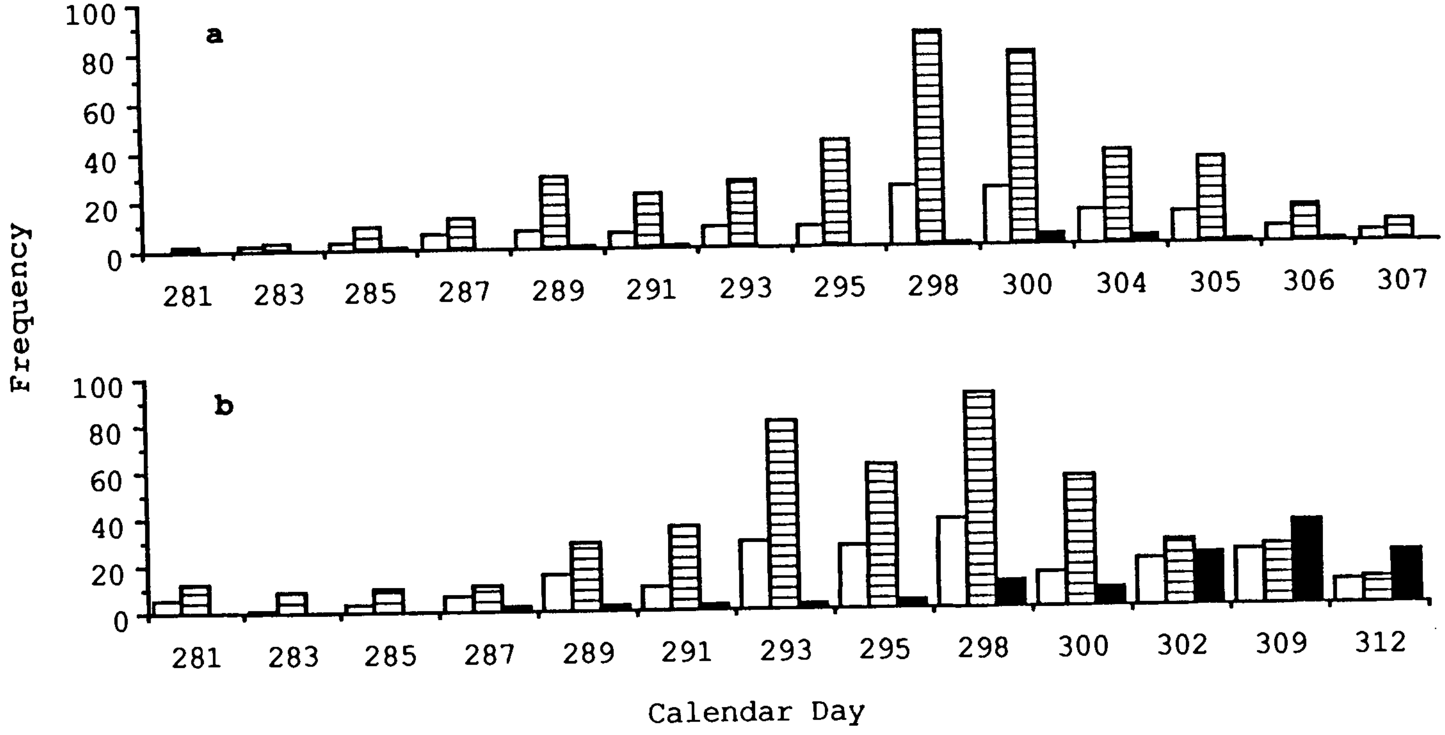


Figure 18. Carcass Recoveries by Calendar Day for Adult Male (White Bar), Female (Hatched Bar) and Jack (Black Bar) Chinook Salmon from within the Study Area during 1984(a) and 1985(b).

Table 15. Frequencies of Jack, Adult Male and Adult Female Carcasses Recovered on the Tagging Weir and Those Recovered Upstream in the Study Area, and Frequencies of Jack, Adult Male and Adult Female Carcasses Recovered Spent or as Prespawning Mortalities on the Tagging Weir or within the Bogus Creek Study Area from October 3 through October 28, 1985.

	Jack	Adult Male	Adult Female	Total
On Weir	41	100	166	307
Upstream	20	110	305	435
Total	61	210	471	742
Prespawning Mortality	9	39	50	98
Spent	52	171	421	644
Total	61	210	471	742

Approximately 67 percent of jack carcasses, 48 percent of adult male carcasses and 35 percent of female carcasses were recovered on the weir. Pair-wise comparisons showed significant differences between weir recovery rates of each group: Jack vs Adult Male - $X^2 = 6.507$, $0.01 < p < 0.02$, 1 d.f.; Jack vs Female - $X^2 = 21.895$, $p < 0.001$, 1 d.f.; Adult Male vs Female - $X^2 = 14.686$, $p < 0.001$, 1 d.f.

Carcass surveys in 1985 also revealed a significant difference in the relative frequencies of spent and prespawning mortalities among jack, adult male and adult female carcasses ($X^2 = 8.158$, $p < 0.025$, 2 d.f., Table 15). Prespawning mortality was 14.8, 18.6 and 10.6 for jacks, adult males, and adult females, respectively (Table 15). Pair-wise comparisons showed that adult males suffered a significantly higher prespawning mortality rate than females ($X^2 = 7.406$, $p < 0.01$, 1 d.f.), but that jacks had an intermediate rate, not significantly different from adult males ($X^2 = 0.247$, $0.50 < p < 0.70$, 1 d.f.) or females ($X^2 = 0.565$, $0.30 < p < 0.50$, 1 d.f.).

DISCUSSION

Behavior on the Spawning Grounds

The behavior of chinook salmon on the spawning grounds of Bogus Creek was similar to that of most other stream dwelling salmonids (Atlantic salmon - Belding 1934; brown trout - Greenley 1932, Jones and Ball 1954; chum salmon - Tautz and Groot 1975, Schroder 1981a and 1981b; coho salmon - Briggs 1953, Shapovalov and Taft 1954; pink salmon - Sheridan 1960; rainbow trout - Greenley 1932, Shapovalov and Taft 1954, Tautz and Groot 1975; sockeye salmon - Schultz 1937, Mathisen 1962, Hanson and Smith 1967). No previously undocumented behaviors were exhibited by chinook salmon on Bogus Creek.

Chinook salmon spawning behavior data collected at Bogus Creek suggested that male size (length) may have been used by females to assess potential mates and by males to assess potential rivals during interactions on the spawning grounds. Furthermore, significant differences in the behavior of reproductive female and male chinook salmon toward males of different relative size were interpreted to reflect female and male assessments of these males as potential mates and rivals, respectively.

During nest construction, the behavior of reproductive female chinook salmon indicated a preference for equal sized and larger males as mates. Reproductive female chinook salmon were more aggressive toward smaller males and less aggressive toward equal sized and larger males. Moreover, these females expressed more courting behaviors toward equal sized and larger males, and less toward smaller males (see Table 6).

Spawning behavior studies of other salmonid species also have suggested a female preference for larger males as mates (Hanson and Smith 1967, Schroder 1981a, 1981b, Semenchenko 1987). Schroder (1981a, 1981b) observed that female chum salmon presented with only "small" males slowed their nest construction compared to when they were only courted by larger males. Similarly, Semenchenko (1987) noted that the duration of female sockeye salmon spawning was extended when only "small" males were present. Schroder (1981a) surmised that by slowing nest construction when only small males were present a female chum salmon increased her chances of being found by a larger male prior to spawning, and in this way attempted to "select" a mate.

During observations of 10 male and 10 female sockeye salmon placed in a pen, Hanson and Smith (1967) found that females attacked small males more frequently than large males. However, Schroder (1981a) observed no difference in the frequency of female chum salmon aggression toward males of different relative size when only one male was paired with each female (n=7).

Although reproductive female chinook salmon appeared to behaviorally "choose" mates based upon male size when all female interactions with males encountered during observations were considered, when only the first interaction between lone reproductive females and new males was analyzed, these females responded aggressively toward new males in 41 percent of such encounters (n=200), regardless of the relative size of the male. It was not determined whether this aggression resulted from the inability of the female to immediately distinguish gender of the new fish, whether the aggression was used by females as a "test" for new males, or whether there was some other reason to be aggressive, but this aspect of behavior warrants further study.

Moreover, just prior to spawning female chinook salmon were not aggressive toward males of any size. This statement is based upon nine focal-female samples in which the females spawned after being courted by equal sized or larger primary males with one or more satellite males in each courting group. Although the lack of aggression toward any male just prior to spawning may have indicated a lack of preference at this point in the spawning sequence, mate selection by these females may have occurred prior to observation. That is, females may have been aggressive toward smaller males while they delayed spawning long enough to attract an equal sized or larger male (see

Schroder 1981a, re female behaviors attractive to male chum salmon). However, one observation indicated that female chinook salmon, indeed, were not or could not be selective of their mates immediately prior to spawning. In this instance the observer scared off the primary male. A satellite male of about 45 cm FL remained near an approximately 80 cm female, courted her for two minutes then spawned with her as the only male.

Observed differences in male chinook salmon behavior toward other males of different relative size appeared to signify that size (length) was used by males to assess rivals. In general, male encounters with larger and smaller males in a spawning group resulted in submissive and aggressive responses, respectively, whereas encounters with equal sized males elicited a more varied response (Tables 9 and 10). Males most often responded by swimming or drifting downstream away from encounters with larger males (65 percent of such encounters), whereas they most often chased or bit smaller males encountered (45 percent of such encounters, Table 9). Behavioral responses to encounters with equal sized males consisted primarily of T-displays (27 percent), nudges or pushes (28 percent) and chases or bites (26 percent of such encounters, Table 9).

If male dominance was size-dependent, as appeared to be the case with chinook salmon on Bogus Creek, then dominance should have been rapidly established between dissimilar sized males. However, when two males were approximately equal sized, dominance was probably not immediately obvious to either male and had to be determined behaviorally. T-displays were more often exhibited toward equal sized males (27 percent of encounters) than toward either smaller (14 percent) or larger males (11 percent). The lateral body view with dorsal fin extended presented by the T-displaying male exhibited his size to best effect. In this way the displaying male may have tried to intimidate his opponent.

Prolonged series of T-displays, occasionally followed by escalation to fighting, were only observed between approximately equal sized male chinook salmon. Schroder (1981a) also found that displays followed by "ritualized fighting" only occurred between equal sized chum salmon males. Moreover, Schroder (1981a) stated that such displays from smaller males were either ignored or responded to aggressively by resident males. Schroder (1981a) allowed single pairs of male and female chum salmon to establish redds and start courting (residents) in individual enclosures, and then added males of different size to see how well and how long resident males were able to defend females.

Although display behavior appeared to be a non-combative means of establishing dominance, displays alone appeared insufficient to resolve a contest in some cases.

However, fighting would use energy that might otherwise be used to search for, court and spawn with females, so escalation to physical "combat" should be avoided if possible (Semenchenko 1986, 1987). Prolonged combat among spawning male chinook salmon was unusual in Bogus Creek.

Primary status was observed to change without fighting, even when the intruding male was approximately the same size as the primary (see, e.g. tagged male 295, Success of Individual Males). The ease of takeover in the case of tagged male 295 may have resulted from dominance being established in a previous encounter. Dominant-subordinate relationships among tagged male chinook salmon, once established, appeared to be maintained throughout most or all of the reproductive life of the primary male (e.g. tagged males 059 and 035, and 059 and 063, Success of Individual Males). Schroder (1981a) observed that resident male chum salmon were able to successfully defend females from new males 90 percent of their size (weight) for 70 to 90 percent of their reproductive life.

Establishment of sustained dominance may have reduced some of the spawning disruptions caused by competition among males. Disruptions caused by male competition at high male to female ratios (greater than 3 males per female) were implicated in female gamete retention in spawning experiments involving pink salmon

(Chebanov 1986), and by increased time to completion of all nests among chum salmon females (Schroder 1981a).

Strategies for Reproductive Success

Male Strategies

There are at least three different means whereby a male chinook salmon might enhance its successful access to reproductive females on the spawning grounds. First, a male might differ sufficiently from the average of the male population in run timing or in timing of gonad ripeness so that competition from other males might be reduced. Second, a male might adopt specific behavioral strategies of interaction with other males or with females that might enhance its mating success. Third, a male might have increased longevity on the spawning grounds, when compared to the average longevity of other males and females, possibly allowing him to find more spawning groups with which he could successfully spawn. This study provided evidence that all these means are adopted by male chinook salmon on Bogus Creek.

Run Timing or Timing of Reproductive Maturity. Jacks, as a group, entered Bogus Creek later than adult males in both 1984 and 1985, and they also appeared to become reproductively mature primarily near the end of each spawning season. The proportion of jacks passing the Fish and Game weir was much higher than for adult males and, since most fish remaining below the weir spawned soon after creek entry, it seems reasonable to conclude that jacks entered Bogus Creek less ripe than adult males. Similar relative run timing has also been observed for Klamath River fall chinook salmon entering Iron Gate Hatchery (Hiser 1987), and for Kamchatka River, U.S.S.R., summer run chinook salmon (Vronskiy 1972). Relative run timing of adults and jacks appears to be stock-specific, however, and in other stocks entry of jacks often precedes entry of adult males (e.g. Elk and Sixes Rivers, Oregon - Downey et al. 1986, 1987; Feather River, California - Schlichting 1987; Eel River, California - Milligan 1987; Scott River, California - J. Hanson, pers. comm.) and in some cases there is no obvious difference in run timing of jacks and adults (fall chinook salmon returning to Mad River Hatchery - Barngrover 1987; spring and fall chinook salmon returning to Trinity River Hatchery - Bedell 1987; Shasta River, California - J. Hanson, pers. comm.).

Delayed reproductive maturation of jacks in Bogus Creek may have allowed jacks to minimize direct competition with large numbers of larger males. One consequence of such late maturation of jacks as compared to adult males, however, was that fewer females were present for potential spawning and the average size of these females was smaller than that of females present earlier in the spawning season.

Adult male chinook salmon entered Bogus Creek and became reproductive at approximately the same time as females. This strategy insured that adult males, particularly the largest males, were present during the period when the potential for obtaining fertilizations was at a maximum based on female numbers.

Behavioral Strategies. Two strategies were employed by male chinook salmon on Bogus Creek in attempting to gain fertilizations during spawning: fighting and sneaking. However, the distinction between the two tactics among male chinook salmon was not as clear as that observed for coho salmon (Gross 1985) or pink salmon (Keenleyside and Dupuis 1988). True sneakers, "males that used 'refuges' to escape aggression from larger males while remaining close to the nest site" (Gross 1985), were not commonly observed among chinook salmon spawning groups. Of the 29 observed spawnings involving more than one male, only one involved a jack in a true sneaker position (i.e. lateral to the female in water too shallow for the primary male), and that jack missed the spawning.

More often, subordinate male chinook salmon took position in an apparently linear hierarchy or a crescent shaped group downstream of the female and primary male.

Some of these males occasionally had rocks or, more often, the tailings of the redd between themselves and the primary male, but they seldom remained stationary behind cover until spawning as did "sneaker" coho salmon (see Gross 1985). Instead, they constantly tried to shorten the distance between themselves and the nest, while the primary male attempted to drive them farther away.

At the time of spawning, satellite male chinook salmon rushed into the nest and attempted to "steal" fertilizations as has been described for other salmonids (Hanson and Smith 1967, Schroder 1981a, 1981b, Chebanov et al. 1984, Gross 1985, Keenleyside and Dupuis 1988). For male chinook salmon, proximity to the female was based upon dominance and was reflected in order of entry into the nest at spawning. Later entering satellite males presumably fertilized fewer eggs than the larger, primary males which usually entered the nest first at spawning. Schroder (1981a) electrophoretically determined that each chum salmon satellite male fertilized an average of approximately 25 percent (range 0-46 percent, n=10) of the eggs deposited by a female when competing with a large male; when two satellites were present they fertilized 30 and 17 percent of the eggs respectively. In a similar study involving sockeye salmon, two satellite males in competition with a primary male fertilized approximately 8 and 2 percent of the eggs deposited by a female (Chebanov et al. 1984). Schroder (1981a) concluded that "...the closer and more attuned a male was to the female the more eggs he was able to fertilize."

The tactic of moving between the primary male and female as they spawned was relatively common among satellite male chinook salmon, especially among the third or fourth males to enter the nest during spawning. Primary male chinook salmon generally entered the nest first or at the same time as the first satellite, so they were likely to release milt before or at the same time as the first satellite. By moving between the female and primary male upon entering a nest, a satellite would be close to any unfertilized eggs and could possibly disrupt the primary male before he completed spawning (see also Schroder 1981a). This may have been the only way a male entering the nest fourth among males at spawning could obtain any fertilizations.

Large male chinook salmon were more direct in their strategy to attain fertilizations. They attempted to gain primary status with reproductive females through displaying (intimidation), or aggression (bites, chases, charge-bites) toward any other males present. Larger than average male chinook salmon were more successful than smaller males in attaining primary status with females (Figure 17). This appeared to be true for large males of other salmonid species as well (chum salmon - Chebanov 1979, Schroder

1981a; pink salmon - Chebanov 1980, 1982; sockeye salmon - Hanson and Smith 1967).

Primary chinook salmon males not only entered the nest before satellite males at spawning, but they also were observed to leave the nest sooner than satellites after spawning, often within a couple of minutes. Keenleyside and Dupuis (1988) found that primary male pink salmon showed the same tendency to leave soon after spawning, whereas satellite males remained longer, sometimes through a second spawning. Once a chinook salmon female spawned, observations indicated that she would not spawn again until her eggs were covered and a new nest was excavated.

If female chinook salmon required 7 to 9 hours to complete a nest (see Female Behavior at Spawning), then large primary males, by leaving soon after spawning, probably improved their chances of spawning again in a short period of time, because their size apparently allowed them to quickly and easily attain primary status with another female (see also, Chebanov 1979, 1980, 1982). Smaller than average sized male chinook salmon appeared less likely to easily find another female near spawning in whose courting group they could establish themselves (Figure 17, see also, Chebanov 1979, 1980, 1982). Moreover, there appeared to be a slight trend toward increasing exclusion from spawning of the lowest satellite in the hierarchy with increasing satellite number (Table

11). For these reasons, it may have been advantageous for an established, smaller male chinook salmon to remain with a single female through all her spawnings.

Longevity on The Spawning Grounds. The limited number of longevity calculations for males precluded determination of any possible relationship between the size of chinook salmon males and their reproductive longevity on the spawning grounds. All other factors being equal, however, males that lived longer on the spawning grounds should have improved their chances of fertilizing eggs by virtue of their remaining reproductive as new females become reproductive, and by outliving their competitors.

The effect of longevity on improving chances for fertilizations was illustrated by the life histories of tagged males 059 and 063 on the spawning grounds. Both were 87 cm and became reproductive at the same time during the spawning period. Male 059 was in primary status during 64 percent of his observations as compared to 34 percent for male 063. However, by virtue of his longer reproductive life (15.5 days) as compared to male 059 (9.5 days), male 063 was estimated to spawn as a primary the same number of times as male 059 (12 times, Table 14). Thus, male 063 was able to wait longer for spawning opportunities than male 059. Longevity on the spawning grounds was also a factor in the equal number of estimated spawnings for tagged males 099 and 380 even though male 380 was observed as a primary or satellite in a higher proportion of observations than male 099 (see Table 14 and Figure 17).

Female Strategies

All female chinook salmon searching for redd sites in Bogus Creek appeared to adopt a strategy of selecting an acceptable, unoccupied area of spawning gravel from what was available when and where they were ready to spawn. No data were collected on the "quality" of redd sites selected by large and small females, or by early and late spawners. Redd location and fredle index data collected by Neilson and Banford (1983) on a stock of chinook salmon spawning in the Nechako River, British Colombia, indicated that the first females on the spawning grounds selected relatively deeper, slower water spawning sites with high fredle indices. These authors concluded that early spawners selected the "best" redd sites because higher fredle indices probably indicated a greater probability of alevin survival to emergence, and deeper water reduced the probability of desiccation or ice scour.

All female chinook salmon on Bogus Creek constructed and defended a single redd. The chinook salmon females observed by Neilson and Banford (1983) also dug single redds. Construction of a single redd allowed a female to protect all her eggs after burial. The large number of female spawners in Bogus Creek made re-excavation of undefended redd sites highly probable; many redds of early spawning females were re-excavated after the females had died. Furthermore, as Piper et al. (1982) state, salmonid eggs become "progressively more fragile during a period extending from 48 hours after water hardening until they are eyed. An extremely critical period for salmonid eggs exists until the blastopore stage is completed." Mechanical shock, such as a new female digging near the eggs, during this stage will kill the eggs, so it would be advantageous for females to protect their redds at least through blastopore closure in the eggs.

The development rate of salmonid egg depends upon temperature and by using Daily Temperature Units (DTU, one DTU equals 1°F above freezing for a 24-hr period) estimates can be made of the time required for eggs to reach different developmental stages (Piper et al. 1982). Donaldson (1955) stated that 200 and 350 thermal units (i.e. DTUs) were required by chinook salmon eggs for the closure of the blastopore and to reach the eyed stage, respectively. In Bogus Creek, at average water temperatures of approximately 10.3 and 10.0 °C during the spawning seasons of 1984 and 1985, respectively, chinook salmon eggs should have reached blastopore closure after about 11 days and the eyed stage after about 14 days during each year.

On Bogus Creek, virtually all female chinook salmon, regardless of size, were able to protect their redds until they were near death, so female redd residency times minus two days for redd construction and spawning were used to represent the amount of time females were able to protect their eggs during development. On average, female chinook salmon protected their eggs through approximately 51 percent (5.6 days/11 days) and 62 percent (6.8 days/11 days) of the time required for blastopore closure in 1984 and 1985, respectively (see Female Postreproductive Stage).

Other studies which addressed female redd defence also concluded that most females protected their redds until they were near death (Hanson and Smith 1967, Schroder 1981a, Neilson and Banford 1983). Researchers studying redd residence times of female chinook salmon have calculated higher average residence times than observed for Bogus Creek females. Neilson and Banford (1983) calculated mean residence times of 15.4 days ± 4.0 days (n=18) and 14.5 days ± 4.0 days (n=29) for female chinook salmon in two study areas in the Nechako River, British Colombia. These authors added one day to individual residence times to account for time on the redd before the first siting and after the last. An overall average residence time of female chinook salmon calculated using data of Neilson and

Geen (1981, Figure 1) from the Morice River, British Colombia was 12.0 days ± 3.2 days.

If water temperatures during early incubation in each of these rivers were similar to those of Bogus Creek (it's likely temperatures were lower than those of Bogus Creek) and two days were subtracted to account for redd construction and spawning, then, on average, females in the Nechako Rivers would have been able to protect their redds through blastopore closure of the eggs, whereas females in the Morice River would have been able to protect their eggs through 90 percent of the period to blastopore closure.

There were several possible reasons why female chinook salmon on the Nechako and Morice Rivers lived longer than those on Bogus Creek: 1) females in these other rivers expended less energy in migration; 2) female competition for redd sites was less intense and this allowed females to live longer (see van den Berghe and Gross 1986); 3) females on spawning grounds in Bogus Creek during 1984 may have been in poorer than average condition due to effects associated with the El Nino event of 1982-1983 (see Hayes and Henry 1985); or 5) water temperature in Bogus Creek may have been warmer at the time of spawning, increasing the metabolic rate of Bogus Creek females.

The only evidence that size might have affected the ability of a female chinook salmon to establish a redd site was that proportionally fewer smaller than average-sized, tagged females spawned within the study area during 1985. One possible reason for this was that larger than average females were better able to establish redd sites in occupied spawning areas. Alternatively, smaller than average sized females may have entered Bogus Creek less ripe and migrated higher in the creek before selecting a nest site (as did jacks).

Implications of Carcass Survey Data for Mark-Recapture Estimation

Carcass surveys have been used to gather data for estimating spawning populations of Pacific salmon (Oncorhynchus sp.) in two different ways. First, live upstream migrants have been trapped and tagged at some point below their actual spawning location, and then recovered at some later date as carcasses on the spawning grounds (see Eames and Hino (1981) for a quick review of this type of study). Second, surveys of the spawning grounds have been used to both mark and recover carcasses (Boydstun 1987). The behavior of chinook salmon on the spawning grounds can result in biases in estimation for each of these methods.

In the first case, when mark sampling is conducted below the spawning grounds and carcasses are sampled for recovery, the behavior of jack, adult male and female chinook salmon just before death results in different recovery probabilities. That is, the probability of recovery of jacks is less than that of adult males, which is less than that of females (see also, Eames and Hino 1981). This invalidates the mark-recapture requirement that each individual in the population has the same recovery probability. However, separate estimates for jack, adult male and female segments of the population would be valid. Unfortunately, recoveries of marked carcasses can be quite low for one or more of these segments.

In the second case, where sampling for marking and sampling for recovery are both conducted on carcasses, mark-recapture techniques may provide valid estimates of the total number of carcasses present within a section of stream. However, carcass numbers are not necessarily well related to the spawning population that produced them because the behavior of chinook salmon, particularly jacks and adult males, may result in their being "lost" from the population of carcasses. Thus, carcass based estimates may have serious negative biases relative to the true spawning populations, especially for jacks and adult males.

Potential bias in estimates of female numbers may be partially or completely offset by the technique of "releasing" tagged carcasses back into the water. Since this technique emulates, to some extent, the circumstances of a female dying on or near her nest, the loss of tagged female carcasses may approximate the loss of dying females to the female carcass population. The technique of releasing tagged carcasses back into the stream does not approximate the behavior of dying males, which probably distribute farther from their last spawning sites than females, so negative biases should result from carcass based marking and recapture estimation of the male population.

Boydstun (1987), reporting on a 1981 carcass mark-recapture validation study conducted on Bogus Creek above the counting weir, noted that modified Schaefer and Jolly-Seber methods resulted in widely varied estimates (both above and below true numbers) of the true spawner number. Estimates varied based upon whether only fresh or all carcasses were marked, and based upon whether jack or adult populations were being estimated. However, recovery rates of carcasses by Boydstun (1987) were consistent with those described in this study: the recovery rate for jacks was significantly lower than that for adults, and the carcass survey indicated that adult males accounted for 38 percent of the adult carcasses (776 of 2,065 carcasses) whereas the weir count indicated that 41 percent (1,113 of 2730 adult fish) were males (a significant difference). Although Boydstun (1987) suggests that misidentification of males at the counting weir may have been partly responsible for the difference, male behavior (distributing male carcasses farther from shallow spawning gravels) may also have contributed to this difference in recovery. These differences in recovery would, on average, result in a negative bias in population estimates.

Potential for Genetically Induced Shifts in Age of Maturity due to Fisheries

The behavioral dominance of large male chinook salmon over smaller males resulting in early nest entry at spawning suggests that large males were more successful than smaller males in obtaining fertilizations, as has been found to be true for other salmonid species (see Schroder 1981a, Chebanov et al. 1984). Moreover, reproductive female chinook salmon were more aggressive toward smaller males than toward larger males, suggesting a preference for larger males. Thus, behavior on the spawning grounds indicated that older, larger male chinook salmon had a reproductive advantage, possibly resulting in genes for older age at maturity and larger size being passed to the next generation at a rate greater than the proportion of large males in the total male population. Although ocean troll fisheries, through their harvest of immature fish, result in shifts of spawning runs toward smaller and younger fish (Ricker 1980, Hankin and Healey 1986), such a reproductive advantage for large males may act to maintain the genes for older age at maturity and large size in the population.

Although spawning behavior may insure continued presence of genes for older age at maturity and large size for male chinook salmon, Ricker (1972) and more recently Hankin et al. (1990) provide evidence that age of male parents has little effect on age of maturation of female offspring. Thus, female age at maturity may decline unless larger and older females realize much greater reproductive success than smaller females.

Female size did not appear to affect the ability of a female chinook salmon to establish or protect her redd. However, in 1985, a higher proportion of smaller than average tagged females moved above the counting weir to spawn. This phenomenon may have resulted from smaller females entering the creek less ripe than larger females, but smaller females also may have been less successful than larger females in securing redd sites among established territories.

Through the spawning season numerous chinook salmon redds were re-excavated by subsequent spawners. If larger female chinook salmon dug deeper nests than smaller females (see van den Berghe and Gross 1984, re coho salmon), then it was probable that nests of larger females survived in greater proportion than those of smaller females.

Large female chinook salmon may have an advantage on the spawning grounds, but whether it is based upon selection of higher quality spawning sites, digging deeper nests or some other factor remains to be determined. Future studies should focus on how female size is related to redd site selection based on gravel composition and potential for scour or desiccation, on nest depth and on success in establishing suitable redd sites among previously established territories. Controlled experiments also should be conducted to determine whether females behaviorally "choose" their mates based on male size and whether this choice breaks down immediately prior to spawning as it appeared to in this study. These studies and electrophoretic analysis of the fertilization success of individual males, especially larger males, competing in controlled situations using a number of male size groups and male to female ratios, should be the next steps toward quantifying the effects that large size has on mating success of chinook salmon.

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