

THE EFFECTS OF BREEDING COMPETITION AND ABIOTIC FACTORS ON THE  
BEHAVIOR AND REPRODUCTIVE SUCCESS OF FEMALE CHUM SALMON,  
ONCORHYNCHUS KETA

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
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The effects of breeding competition and abiotic factors on the behaviour  
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## ABSTRACT

In this thesis I examine the effects of intra and interspecific breeding competition on the survival, reproductive success and behavior of female chum salmon (Oncorhynchus keta) breeding in Walker Creek, Vancouver Island, British Columbia.

Spawners successful in territorial contests tended to be robust (large condition factor and snout length) and large in size. Gravel scour was an important source of egg mortality and large, robust females tended to occupy nest sites less likely to be scoured. Consequently there was selection of greater snout length, body size and median fin length. Age and growth of female chum salmon were estimated from scale circuli patterns. Chum salmon females matured on average at age 3.6. A demographic life history model predicted maturation at age 3.3. Those females maturing at age 5 (1.6%) and age 4 (54.4%) were larger than those maturing at age 3 (44%), but had grown more slowly during their ocean residence.

High female density was associated with a longer upstream migration distance, higher egg retention, and lower nest site porosity, a correlate of egg survival. Females arriving to spawn early in the season retained fewer eggs, and defended their nests for a longer period than later arrivals.

Female chum salmon in Walker Creek experienced interspecific breeding competition from female coho salmon by nest superimposition, although at a low frequency because of spatial

segregation of spawning sites. Chum salmon spawned in larger pools with slower water velocity and warmer incubation water than did coho salmon. Chum salmon spawning in areas more typical of coho salmon experienced high egg mortality, possibly as a result of cool incubation temperatures.

I also compared the accuracy of different methods of estimating salmon escapement to Walker Creek. Visual counts of spawners and measures of spawner residence time were major sources of error in some of these estimates.

## QUOTATION

It was almost impossible to desire a better view of the fish than we had during these two days. Some results of these observations did not agree with my former beliefs nor with what I thought I had seen in earlier years. We saw practically no fighting among the males, and very little fear or jealousy. The milting of the cock fish was done very quietly, and, as far as any movement showed, very seldom. For longish periods the females were alone, yet went on spawning busily. It seems to me that there is room for a lot of accurate observation before we shall be very sure of what really does happen in these wintry waters of ours.

A.H. Chaytor (1910)

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## INTRODUCTION

Competition is thought to be a major factor influencing the evolution of many characteristics of organisms. Where heritable variation in traits corresponds to differences in reproductive success and mortality, natural selection may mold morphology, behavior and life history (Endler 1986).

In this thesis I investigate breeding competition in Pacific salmon. While there have been previous studies on this subject they have been confined to a single species, and primarily to a single population (van den Berghe and Gross 1984, 1986, 1987). Hypotheses previously examined in these studies need to be assessed in other populations and species before they can be more widely accepted.

During that portion of their life history spent in fresh water, female chum salmon (Oncorhynchus keta, Walbaum 1792) reproduce and experience mortality from both competitive and abiotic factors. Female breeding competition causes mortality to eggs through nest dig-up (McNeil 1966) and by delaying spawning, which in turn causes egg retention (Schroder 1973). Abiotic factors such as low dissolved oxygen, extreme low or high temperatures, and nest scour, which crushes eggs by moving the gravel they are buried in, all cause mortality to incubating salmon eggs (Neave 1953).

Natural selection requires heritable variation in traits in order to proceed. The body size and morphology of coho salmon (Oncorhynchus kisutch) are variable and selected for by mortality on eggs caused by female competition (van den Berghe and Gross 1987). However, among female chum salmon, body size does not confer an advantage during breeding competition (Schroder 1973). In the first chapter I examine whether breeding competition among female chum salmon causes natural selection for increased body size, increased morphological trait size, and age. In addition I quantify how the physical characteristics of individual female chum salmon influence how abiotic factors such as dissolved oxygen, water temperature and nest scour affect the survival of their progeny, and how these relationships are influenced by female competition.

Among salmonids growth rate is frequently negatively correlated with age at maturity (Alm 1959, Ritter 1975, Thorpe 1975, Helle 1979, Bilton et al. 1982). Another topic covered in Chapter 1 is the relationship of age with body size and fecundity. Age at maturity may be a mixed evolutionarily stable strategy (mESS), where all ages have the same fitness, or a conditional ESS, where ages have different fitness but females make the best of a bad situation (BBS) by maturing at a particular age. Whether age at maturity among female chum salmon is best explained by a conditional or mixed ESS is discussed.

All else being equal, behaviors that respond to changes in both the competitive and abiotic environment in a way that

minimizes mortality will be selected for. Female competition can increase egg mortality by forcing some females to use low survival spawning sites (van den Berghe and Gross 1987). However, McNeil (1966) found that the mean survival associated with the spawning site choices of pink salmon (O. gorbuscha) did not change with changing female density. Different female salmon behaviors could co-exist in a mESS where females have equal fitness. Some researchers have hypothesized that early arrival to spawn might lead to a higher rate of nest dig-up (McNeil 1962), however female nest defense might exhibit temporal patterning in response to the increased risk of nest dig-up. In Chapter 2 I examine how female chum salmon behaviors such as spawning habitat selection, the length of nest defense, and arrival date to spawn respond to competition for nest sites and to abiotic factors. In addition I measure the mortality that female competition and abiotic factors cause the eggs of females performing different behaviors.

Interspecific breeding competition among Pacific salmon has rarely been investigated on the population level (McNeil 1962, Smirnov 1976, Crone and Bond 1976), and even less frequently on the individual level. The high density of spawning salmon found in rivers suggests that there is ample opportunity for interspecific breeding competition to occur; alternatively there could be temporal or spatial segregation of spawning. In Chapter 3 I investigate interspecific breeding competition between chum and coho salmon (O. kisutch), and examine both segregation of



spawning microhabitat and species adaptations to the spawning environment.

All studies were conducted within a single stream, however, I consider data from other populations and species of Pacific salmon when considering evidence for and against hypotheses. Finally in the appendix I compare different methods of estimating populations of spawning salmon (escapement) and illustrate how salmon behavior affects the accuracy and precision of these estimates.

### *Chum and coho salmon*

The species chosen for this investigation belong to the genus Oncorhynchus and are endemic to the North Pacific Ocean. There are at least six species with spawning populations distributed around the North Pacific rim (Jackson 1963); in Japan a seventh species is recognized (Machidori and Kato 1984). Chum salmon have the widest natural range of all the Pacific salmon species and occupy almost all of the subarctic region of the North Pacific Ocean (Shepard et al. 1968). They can be found throughout the North Pacific Ocean north of 40° North latitude, the Bering and Beaufort seas and the southern Arctic Ocean from 130° East longitude east to 135° West longitude. The species is anadromous and reproduction occurs in freshwater rivers along the coast of North America from Sacramento, California north to the MacKenzie River, Northwest Territories and along the coast of Asia from the Tone River, Honshu, Japan north to the Lena

River U.S.S.R.. (Bakkala 1970). Migration distances in freshwater vary from less than 1 km to over 2500 km.

Fertilization among chum salmon occurs June to January (Sano 1966). Eggs, shallowly buried in the substrate of freshwater streams, develop into alevins and then into fry, which leave the substrate from March through June to assume a free-swimming existence (Bakkala 1970). Fry may remain in freshwater for several weeks, but there is no recorded instance of overwintering, and fry commonly migrate to saltwater immediately after emerging from the gravel (Bakkala 1970). Juvenile chum salmon occupy estuarine habitats for periods from a few days to 4 months after which they migrate to the North Pacific ocean and become widely distributed (Neave et al. 1976, Healey 1980, Bax et al. 1980, Hartt and Dell 1986).

Chum salmon spend most of their life in the open North Pacific Ocean where they feed predominantly on euphasids, amphipods, copepods, decapod larvae, pteropods, squid and small fishes (Neave et al. 1976). Adults reach sexual maturity 2 to 7 years after fertilization (Sano 1966) with ages 3,4 and 5 being the most common, age 7 fish are rare and age 2 fish are usually males. Adults migrate from the North Pacific ocean to the freshwater stream of their birth to reproduce. The maximum recorded body weight is 20 kilograms (Lovetskaya 1948).

Chum salmon show a high fidelity to their birthplace: straying to other streams occurs at low frequencies (Neave

1966). Chum salmon spawn in over 880 streams in British Columbia (Aro and Shepard 1967).

Adult entry into freshwater occurs from June to January although later maturation can occur (Wickett 1964). Both sexes undergo morphological transformation: the body becomes laterally compressed and the scales become embedded in the skin which thickens and becomes pigmented (Jordan and Evermann 1896). The snout lengthens through the enlargement of the maxillary, mandibular and premaxillary bones to which the teeth ossify, creating kypes on both the upper and lower jaws (Vladykov 1962). Females excavate depressions in the substrate into which they deposit their eggs (Kuznetsov 1928, Myren et al. 1959, Vasilev 1959). Fertilization by males occurs during egg deposition, and the mating system is polygamous, with the existence of alternate male mating strategies (Kuznetsov 1928, Hunter 1959, Strekalova 1963, Chebanov 1979, Schroder 1973). After spawning, females cover deposited eggs with substrate and guard the nest for a period from 5 to 30 days (Mattson and Rowland 1963, Strekalova 1963).

Coho salmon, like chum salmon, are semelparous and anadromous and reproduction occurs in freshwater streams in both Asia and North America. Coho salmon are less widely distributed than chum salmon, ranging from Monterey Bay, California (Briggs 1953), north to the Nome River in Alaska, whereas in Asia they are found as far south as Hokkaido Island Japan north to the Anadyr River in Kamchatka (Godfrey et al. 1975).

The life history of coho salmon from fertilization to emergence from the gravel is similar to that of chum salmon, however, after emergence most coho salmon remain in freshwater for one or two winters, although a few spend 3 or even 4 winters (Godfrey et al. 1985). Some coho salmon migrate directly to sea after hatching, however survival of this life history type in some streams is negligible (Crone and Bond 1976).

Emigration from fresh to saltwater occurs early in the year (mid-April to mid-June) (Crone and Bond 1976) and upon arrival to saltwater, British Columbia stocks of coho salmon migrate northward within continental shelf waters. Substantial numbers of coho salmon remain in inshore waters (e.g. Strait of Georgia, Juan de Fuca Strait), however, some coho salmon have a migration pattern similar to that of chum salmon (Hartt and Dell 1986). These two migration types have been called 'ocean' and 'inside' types, analogous to the ocean and stream type chinook salmon (O. tshawytscha), although the link between freshwater type and ocean habit among chinook salmon (Healey 1983) has not been made for coho salmon. The predominant prey of coho salmon are squid, small fishes, euphasids and amphipods (Pearcy et al. 1983).

The ocean life of coho salmon is 13 to 18 months long, so coho spend only one winter at sea (Godfrey et al. 1975), and some male coho salmon return to spawn after only 6 to 9 months in the ocean (Shapavolov and Taft 1954). Coho grow the most quickly of all Pacific salmon (Hartt and Dell 1986) and attain typical weights of 2.7 to 5.4 kg: the maximum recorded weight is

14 kg (Hart 1973). Spawning occurs from October (Crone and Bond 1976) to January (Shapavolov and Taft 1954) and in British Columbia occurs in over 970 streams (Aro and Shepard 1967).

Chum and coho salmon are economically important species in British Columbia where the average catch from 1980-84 was 11.4 and 9.01 thousand metric tons respectively (Fisheries and Oceans Canada 1984). This represents a landed value at 1987 prices of \$18.2 million (\$0.60 lb) for chum salmon and \$19.3 million (average of \$0.82 round and \$1.15 troll) for coho salmon. Chum salmon are very important internationally and the total catch of all nations reached a historical maximum of 304 thousand metric tons in 1936 (Salo 1987), however more recently (1952-1976) catches varied from 65 to 169 thousand metric tons (INPFC Secretariat 1979). In British Columbia coho salmon are the mainstay of a huge saltwater sports fishery which involves over 365,000 anglers and in Georgia Strait alone attracts a fishing fleet of 100,000 pleasure boats (Argue et al. 1983).

### *Populations*

In both the scientific and common literature authors use the term "run" to describe the movement of mature salmon from the marine environment to a spawning stream. A "run", therefore, is a temporal and spatial aggregation of sexually mature salmon. It may be composed of one or many stocks. A stock is a reproductively discrete unit, a population of salmon that sustains itself over many generations and maintains a

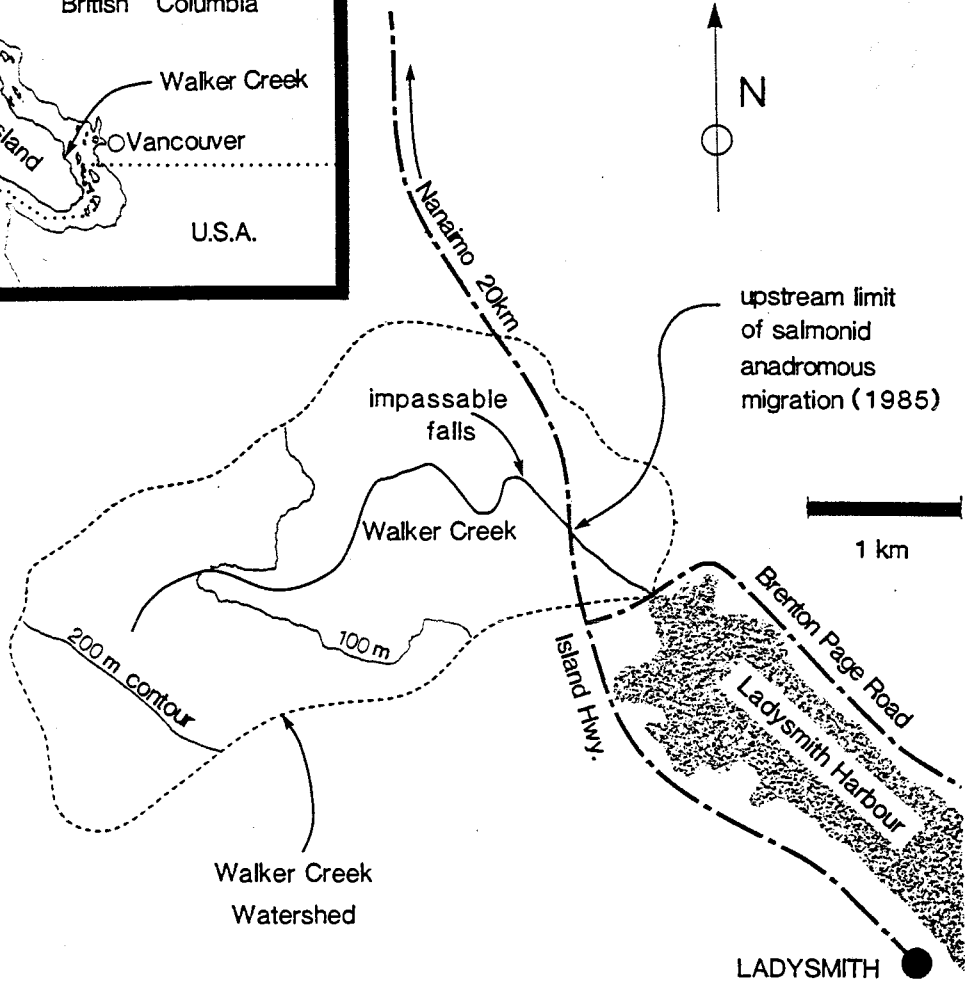
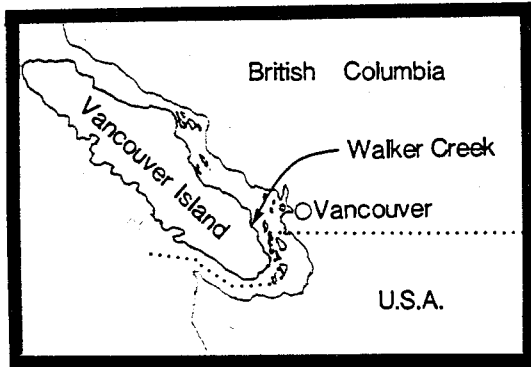
Castle-Hardy-Weinberg equilibrium (Booke 1981). The temporal and spatial aggregation of spawners in a run allows for a high rate of exchange of genetic material among the stock and this in turn results in a high degree of genetic relatedness among the spawners as well as reproductive isolation from other runs of spawners. Reproductive isolation promotes adaptation to local conditions and as a result, a higher absolute fitness (Ricker 1972). Spatial aggregations of spawners are maintained between generations by the behavioral mechanisms of spawning site imprinting and homing (Horrall 1981).

### *Study area*

Field studies were conducted at Walker Creek, 21 km south of Nanaimo, British Columbia, Canada. Walker Creek enters saltwater at 49° 01' 36'' north latitude, 123° 51' 20'' west longitude.

Walker Creek is a second order stream with a discharge during the fall months (season of greatest precipitation) ranging from 0.03 m<sup>3</sup> sec<sup>-1</sup> to 0.65 m<sup>3</sup> sec<sup>-1</sup> (1985-1986). The watershed covers 7.6 km<sup>2</sup> and rises to 452 m above sea level; 3.5 km<sup>2</sup> (51 %) of the watershed lies 100 m or more above sea level 0.9 km<sup>2</sup> (12 %) lies above 200 m. The upper portion of the creek drains the steep northeast slope of Mt. Hayes after which it flows onto a bench with elevations between 50 m and 100 m above sea level. Further downstream the creek flows through a steep canyon with waterfalls after which it enters a coastal lowland. The creek then meanders for 1200 meters and enters saltwater at

Figure I.1: The Walker Creek watershed, British Columbia.





the northwest end of Ladysmith Harbour.

The watershed lies on the western edge of the coastal lowland adjacent to the Georgia depression and has a surficial geology of primarily marine and glacio-marine deposits with some terraced fluvial Capilano sediments (Fyles 1963). The watershed is located in the drier maritime subzone of the coastal douglas fir biogeoclimatic zone, however, logging and agriculture activity have removed the native vegetation and the present plant species associations are more indicative of the drier maritime coastal western hemlock biogeoclimatic zone (Klinka et al 1979). The vegetation of the watershed is dominated by the following tree species: Douglas fir (Pseudotsuga menziesii), Western hemlock (Tsuga heterophylla), broadleaf maple (Acer macrophyllum), and Western red cedar (Thuja plicata).

The climate in this area is typified by warm dry summers and mild wet winters (Klinka et al. 1979). Drought conditions during the summer and early fall months are frequent, however surface runoff is supplemented by groundwater flow from the Cassidy aquifer which provides year-round flow to Walker Creek (Smith and Pratt 1980). Precipitation and temperature are measured on the northern perimeter of the watershed at the 'Nanaimo A' federal climatological station (49° 03' N, 123° 52' W). From 1951 thru 1980 the mean annual precipitation was 1103 mm and the wettest months were November (161 mm) and December (202 mm) while the mean annual air temperature was 14.6 °C, with November averaging 1.2°C and December averaging 1.5°C (Atmospheric

The watershed is primarily second growth forest with some agriculture and urban development. Where the creek enters saltwater at Ladysmith Harbour a sawmill operation occupies a portion of the estuary and most of the intertidal area surrounding the estuary is used for log storage.

The present fish fauna of Walker Creek is composed of chum salmon, coho salmon, cutthroat trout (Salmo clarki), coast range sculpin (Cottus aleuticus), prickly scuplin (C. asper), and the three-spined stickleback (Gasterosteus aculeatus).

The creek is accessible to anadromous salmonids from tidewater upstream for 750 meters where a steeply sloped culvert prevents upstream passage at some water levels. Historically adult chum and coho salmon migrated upstream of this point, (A. Westby pers comm) however presently only coho salmon make the migration and then only when discharge is high. A 3 m high falls is located 1200 meters from tidewater and it appears impassable to salmon.

## CHAPTER I

### NATURAL SELECTION OF AGE, MORPHOLOGY AND BODY SIZE OF FEMALE

#### CHUM SALMON

##### Introduction

The presence of variation in any trait prompts us to ask whether different trait values have equal fitness. Female chum salmon age at maturity ranges from 2 to 7 years (Bakkala 1970) at sizes, in Southern British Columbia, from 461 to 690 mm postorbital-hypural length (Beacham and Murray 1985b). Mean and variance in body size, morphology and age differ among populations (Birman 1956, Sano 1966, Gorshkov 1979, Beacham 1984b).

In this chapter I examine the way in which natural selection affects body size, morphology and age at maturity of adult female chum salmon. Natural selection is measured during the life history episodes of growth (fecundity), adult freshwater survivorship, competition for nest sites, scour mortality, and incubation success.

The importance of body size in female Pacific salmon has been the subject of considerable research in the past decade. While the positive effect of female body size on fitness as a result of its effect on fecundity is well recognized, the advantage of increased body size beyond the fecundity effect is in dispute. Some studies have demonstrated that increased body

size imparts a higher fitness as a result of its advantage in breeding competition (van den Berghe and Gross 1986, 1987) while other studies have found no directional selection for body size (Holtby and Healey 1986) or no advantage to body size in breeding competition for nest sites (Schroder 1981). Fecundity appears to be sacrificed for increased body size in some cases (Healey and Heard 1984, Healey 1987) but not in others (Healey 1986). Hartman (1969) hypothesized that the evolution and maintenance of large size in salmonids is a product of both breeding competition and the stream environment. Body size is positively correlated with stream size suggesting that in small streams small body size is favored (Beacham 1984b, Beacham and Murray 1987a, Rogers 1987). Evidence exists for selection favoring small body size in some species as the result of mortality from commercial fishing (Peterson 1954, Ricker 1981) and predation by bears (Konovalov and Shevlyakov 1978).

The effect of variation in morphology on fitness has also recently been examined by some researchers. The length of the snout (referred to as the kype by some authors), which is used in breeding competition, was positively correlated with fitness during breeding competition among spawning female coho salmon (van den Berghe and Gross 1987). There is evidence from comparative studies that morphological differences between populations are a consequence of selection from both the riverine environment (Taylor and McPhail 1985a, Taylor and McPhail 1985b, Fleming and Gross 1987a) and breeding competition

(Fleming and Gross 1987a).

Body size increases with age, as does the cumulative probability of mortality (Ricker 1976), and consequently the increase in fitness gained by older fish as a result of their larger size is discounted by reduced survivorship. Charlesworth (1973) demonstrated that in any age-structured, diploid, random mating population, a non-recessive mutant which increases  $r$ , the intrinsic rate of increase, will be selected for. Based on a demographic model, Bell (1980) showed that in a semelparous population fitness is maximized when the instantaneous rate of change of fecundity equals the instantaneous rate of change of mortality. Examination of the life history of several species of Pacific salmon suggests that maturity is delayed beyond that predicted by demographic models, presumably in order to achieve the fitness benefits imparted by larger size (Healey 1986, 1987). However, the age of maturation among salmonids appears to be phenotypically plastic as maturity is delayed when growth is poor (Alm 1959, Ritter 1975, Thorpe 1975, Helle 1979, Bilton et al. 1982), suggesting that age at maturity may be a conditional strategy.

Given the above considerations, one working hypothesis of this study was that larger female chum salmon should have a greater fitness than smaller females. This is because larger females lay more eggs and have greater competitive ability so that they obtain nest sites of higher survival value. Under certain conditions, however, large size should be

disadvantageous, particularly in small streams where shallow water depths could decrease the swimming ability of larger females, inhibiting spawning and increasing the risk of predation.

A second working hypothesis was that females with robust morphologies (large condition factors and large relative fin and snout lengths) should have greater fitness during breeding competition as a result of their superior competitive ability. The faster burst swimming speed of robust morphologies (Webb 1977, 1978) suggests they will suffer a lower risk of predation. Their ability to negotiate small watercourses might, however, be less than that of more fusiform morphologies. In shallow water robust morphologies would experience more frictional drag since a larger proportion of their body would be above water. Consequently the ability of robust morphologies to negotiate small watercourses might be less than that of fusiform morphologies and as a result their risk of predation might be greater.

Working hypotheses regarding age at maturity are as follows. If fitness is frequency independent, then demographic models should predict the observed age at maturity. However, if fitness is frequency dependent, then game theory (Maynard Smith 1982) will better predict the pattern of age at maturity. Myers (1986) suggested that female age at maturity could be a mixed ESS where all females had equal fitness. However, age at maturity would be a conditional ESS if ages have unequal fitness but phenotypic

plasticity of maturation is more fit than any single age at maturity.

## Methods

Field studies were conducted on a population of wild female chum salmon at Walker Creek. Behavioral studies were conducted from November 1985 to early January 1986. Females were collected for morphological measurements in fall 1985 and 1986.

A fence to capture adult salmon was constructed across the stream near tidewater. Upon capture female chum salmon were anaesthetized in 2-phenoxyethanol and length ( $\pm 0.5\text{cm}$ ) and weight ( $\pm 0.05\text{ kg}$ ) measured. Scales were taken from between the dorsal fin and lateral line and read for age by the author and the Fish Ageing Unit, Biological Sciences Division, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.. Partially spent, spent, and injured females were excluded from behavioral and morphological analyses since their fins were likely eroded during the spawning process or through injury, such that measurements were not comparable with unspawned, uninjured females. All females were tagged with an individually numbered Peterson disk tag anterior to the dorsal fin.

Fence checks were made 86 times during the study at an average rate of once every 8.0 hours (usually at 0900, 1600, and 2200 hrs.). Additional checks made on an intermittent basis were not recorded if fish were not present. The true time of arrival for each fish was taken as halfway between checks. The measurement error involved in assessing the time of arrival to the fence was  $\pm 4.00$  hours.



Fourteen females in 1985 and 18 females in 1986 were selected from the population upon entry to the stream and sacrificed in order to determine fecundity, egg weight, and gonad weight. Each female was weighed, her ovaries were removed and weighed to the nearest gram and the number of eggs in the ovaries was estimated by volume. Mean egg weight was calculated as the ovary weight divided by the fecundity. Because ovaries contain ovarian fluid, this method overestimates true egg weight.

Total length, snout length, the distance from the posterior edge of the orbit to the posterior edge of the hypural plate (postorbital-hypural length), caudal fin length, and the length of the anal fin (Hubbs and Lagler 1958) of 99 females were measured with calipers. In 1986 the dorsal fin height was also measured. Since the size of body parts relative to body size was of interest, the morphological measures were adjusted for the postorbital-hypural length as follows:

$$M_t = M_o (\bar{L}/L_o)^b ;$$

$M_t$  = adjusted morphometric measurement;

$M_o$  = observed morphometric measurement;

$\bar{L}$  = overall mean length for females combined for the entire population;

$L_o$  = observed length;

$b$  = regression coefficient for the population of  $\log_e M_o$  on  $\log_e L_o$ .

This methodology follows Ihssen et al. (1981). The body condition factor calculated was  $(\text{weight}/\text{length}^3) \times 100$  (Fulton 1902). Condition factor is a morphological variable that

measures body robustness (Gershanovich et al. 1986).

Age and growth of female chum salmon was estimated from scale circuli patterns. Scale annuli are laid down in the winter and early spring months each year, roughly at 12 month intervals after hatching (Bilton and Ludwig 1966). Fish were aged according to the number of annuli present and annuli were identified according to the criteria of Lalanne and Saftsen (1969). Ages presented in this paper are the number of annuli present on the scale plus 1 following Gilbert and Rich (1927). Fish ages were corroborated with readings by the Fish Ageing Unit, Biological Sciences Division, Department of Fisheries and Oceans. The distance between annuli ( $\pm 0.01\text{mm}$ ) was determined as per Bilton (1985), however, a video-enhanced microscopic image of the scale was measured with a micro-computer assisted caliper. Analysis of growth was by scale increment following Weisberg and Frie (1987). Instantaneous growth rates were calculated following Ricker (1975) where instantaneous growth =  $\log_e (\text{size}_t / \text{size}_{t-1})$ . Back-calculation of body weight from scale increment widths was performed using the regression method. Although the Dahl-Lee method is recommended (Gutreuter 1987), back-calculation was restricted to 1 annulus prior to capture to minimize error in the regression method and from Lee's phenomenon.

Stream temperatures were measured 3 times daily, coincident with fence checks. A thermograph monitored stream temperatures when temperatures could not be measured on a daily basis. Staff guage measurements were taken daily from a permanent staff guage

installed at Brenton Page Road. A discharge versus staff gauge function was established during 1985.

Observations of female chum salmon were made daily from the arrival of the first female until all females had died. Females were observed from 1 to 10 times daily, with an average of 1.8 observations female<sup>-1</sup> day<sup>-1</sup> (1822 observations total). In major spawning areas a grid was established to allow accurate measurement of fish location. Behavioral observation and consultation of references (Schroder 1973, Tautz and Groot 1975) allowed me to categorize female salmon behavior. Table 1.1 describes these behaviors. The freshwater lifespan of female chum salmon can be divided into 7 sequential periods dominated by a specific behavior: migration, holding, nest digging, spawning, defending, evicted, and dying. These periods tended to be, but were not always, discrete.

After each female died, its carcass was examined for signs of recent predation (fresh blood, external wounds, non-waterhardened eggs, moist skin) and was dissected to determine the number of eggs retained.

The frequency of competitive interactions between females was recorded during observations, as was the duration of observation, thus the number of interactions in the observation period could be determined. The length of the the observation period was determined by logistics (number of observers available and time requirements of fish tagging) and was usually 5 minutes in duration; if longer the number of interactions was

Table 1.1:

Categorization of behavior patterns of female chum salmon as determined by Schroder (1973) and modified by the author.

Behavior Pattern	Description
Digging	A series of body flexures performed while the female is turned on her side.
Exploratory or test digging	Digging performed randomly prior the selection of a nest site.
Pre-spawn digging	A series of digs performed in the same location to construct a nest.
Post-spawn digging	A series of rapid, violent digs located upstream of the nest.
Displacement digging	A digging where female skips across the substrate as a result of her body flexures. These digs do not occur on the nest, are frequently outside of the female's territory and sometimes are located on other female's nests. These digs are usually associated with aggression to other females and often follow or are followed by agonistic behaviors to other females.
Spawning	The female lowers herself into the nest depression for 4 to 10 seconds and lies motionless except for quivering of her body. Accompanied by 1 or more males during this activity.
Agonistic behaviors	Consist of biting of the head, operculum, caudal peduncle or caudal fin. An aggressive female may hold her grip for up to 10 seconds and occasionally shake her body. The attacked female or male usually reacts by attempting to swim away and once free, retreats away from the aggressor.

standardized to the frequency per five minute interval.

Contests between females were observed and both the territorial status of participants and the outcome of the contest were recorded. Contest participants were classified based upon their previous behavioral history in the stream as either non-territorial (no history of nest construction or spatially-centralized defensive activity) or territorial (history of nest building and nest defense in the area under contest).

The outcome of a contest was classed as either a win, a draw or a loss. A win or a loss was scored when one female (the winner) forced the other female (the loser) to retreat 2 or more meters away from the holding positions of the females prior to the interaction. A draw occurred when neither female was displaced as much as 2 meters. Two meters was chosen arbitrarily as the criterion of displacement because of the 1 meter spacing of the observation grid lines and because it allowed maximum resolution for a spatially mobile event such as a contest. Even though objective criteria for the classification of contest outcomes were established, the process was not without subjectivity. As a result, contests where a victory could not be determined with confidence were classed as draws.

Nest superimposition was detected by recording nest site locations on a map and measuring the overlap. Because chum salmon spawning activity occurs with equal intensity around the clock (Tautz and Groot 1975), it was not possible to observe all

nest constructions, evictions, or superimpositions. However, because all females were individually marked and defend only their own territories (present study, Schroder 1981), nest superimposition could be identified whenever a nest site was defended by a female other than its original owner.

If nests are superimposed, mortality to the previously buried eggs may occur if the eggs are shocked or released into the stream where they are prone to damage and predation. I considered dig-up to have occurred in established nests if the following three events were observed:

- a. A new female occupied the nest site previously occupied by another female.
- b. The new female superimposed her nest on the previously constructed nest by at least 50%.
- c. Free drifting red or pink colored eggs were found immediately downstream.

These criteria for the detection of nest dig-up are identical to those used by van den Berghe and Gross (1984) and assume that mortality during nest superimposition occurs primarily from nest dig-up.

The depth of egg burial was determined by two independent methods. First, by placing a measuring rod into the center of the nest immediately after egg deposition but prior to covering of the eggs, the egg burial depth was defined following van den Berghe (1984) as the maximum distance from the top of the water column to the deepest place in the nest, minus the distance from the top of the water column to the top of the undisturbed

substrate around the nest. In the second method substrate samples were taken at known nest sites by the freeze-core technique following Ryan (1970). The distance in centimeters from the top of the substrate core to the centre of the egg cluster was defined as the egg burial depth.

Substrate samples were taken from Walker Creek using the freeze-core method on January 29<sup>th</sup> and 30<sup>th</sup> 1986. Samples were taken at locations where female chum salmon were seen constructing nests and defending them. Samples were removed from the substrate and then split horizontally into two subsamples of equal size - one representing the top 15 cm and the other the bottom 15 cm of substrate. In each sample the number of eggs present and the proportion dead was estimated. The opaque yellow-orange color of dead eggs allowed them to be easily differentiated from live eggs which were a translucent orange-red color even when frozen. Substrate samples were retained in plastic bags for analysis by the author at the Gravel Laboratory, Department of Fisheries and Oceans, North Vancouver B.C..

Substrate composition was measured by sieving dried substrate samples into size fractions, and weighing them (Scrivener and Brownlee 1982). These data were used to calculate the fredle index, a measure of substrate porosity which is positively correlated with egg to emergence survival of coho salmon (Lotspeich and Everest 1981).

The temperature and dissolved oxygen of both stream and intra-gravel water were measured at known chum salmon nests. Preliminary sampling in October 1985 showed that negligible change in intra-gravel water temperature occurred from 20 to 50 cm below the substrate surface, the depth within which chum salmon eggs are often found (Tripp and Poulin 1985). Further, Hartman and Leahy (1983) report that, where intra-gravel temperatures differed widely from those in the stream, most of the temperature gradient occurred in the top 20 cm of the substrate. Consequently, temperature and dissolved oxygen were measured 20 cm below the substrate surface. Temperatures were taken by a Yellow Spring Instruments (YSI) telethermometer while dissolved oxygen was measured by extracting intra-gravel water from 20 cm below the substrate surface with a 1 liter steel syringe (Ryan 1972) and measuring the dissolved oxygen with a YSI model 54 oxygen meter. Intra-gravel temperatures were taken five times during the period of intra-gravel juvenile development (December 10, 1985 and January 31, February 12, March 10, and April 15, 1986), while oxygen measurements were taken twice on (January 29 and April 15, 1986).

High water discharges, which can cause the displacement of gravel (scour), occurred in Walker Creek prior to gravel sampling and visual evidence of gravel scour was present on January 30, 1986. As a result, egg burial depths measured from gravel cores may be incorrect.

Intra-gravel temperature and dissolved oxygen at 20 cm depth collected in late January 1986 will be used in analyses



comparing the characteristics of incubating water at different nest sites. This is approximately the mid-point of the development period from fertilization to hatching (71 day period at 8°C (Tallman 1986) and temperatures and dissolved oxygen measured at this time are still representative of incubation conditions throughout egg development because intra-gravel conditions changed little during the season.

All statistical analyses were performed using the Statistitcal Package for the Social Sciences (SPSS Inc. 1983). Arithmetic mean least sum of squares regression analysis was used to determine the significance of relationships between continuous dependent and independent variables. The variance explained in regressions is reported using the adjusted r squared statistic,  $r_a^2$ . The normality of variance assumption of linear regression analysis was tested using the Kolmogorov-Smirnov test for normality at different values of the independent variables while the homogeneity of variance assumption was tested with Kendall's tau-b statistic from the rank correlation of the absolute value of the residual and the value of the independent variable. Coefficients of variation were tested by t-test following Sokal and Braumann (1980). Tests of significance were two-tailed except where a priori predictions were made, then one-tailed tests were used. Alpha levels for all tests were 0.05.

Geometric mean regression was used when the data fulfilled the criterion of Ricker (1973) for suitability, but only when predicted values from the regression equation were used for

further analysis, since it was in these situations that the use of the geometric mean regression instead of the arithmetic mean regression would have a significant effect on further analysis.

Logarithmic transformation of data was performed to normalize data for parametric tests, or when theory suggested variables were related by power functions.

For comparisons of groups of morphological variables, logarithmic transformation was performed following Lande and Arnold (1983), but only when the ratio of variances of the untransformed variables was closer to the ratio of their squared means than to the ratio of their means, as recommended by Bryant (1986). The correlation matrix of untransformed traits and the transformed variances of compared traits were examined for homogeneity prior to transformation as recommended by Bryant (1986), although they were not tested statistically.

Multivariate as opposed to univariate selection analysis was used to distinguish between selection on and for traits. Selection may act on a trait without actually selecting for it solely because of its correlation with traits being selected for (Lande and Arnold 1983). Selection intensities are measures of selection on traits while selection gradients are measures of selection for traits and both will be calculated here. Selection differentials and gradients of traits were calculated following Lande and Arnold (1983) and were standardized by dividing by the standard deviation of the character distribution (see also Endler 1986).

Direct discriminant function analysis was used to determine which variables best distinguished between pre-determined groups. The significance of discriminant functions was tested using an approximate transformation of Wilk's Lambda to the F statistic (SPSS Inc. 1983). Pooled within-groups correlations between discriminating variables and canonical discriminant functions were compared to identify the relative discriminatory power of different variables. Normality of independent variables was tested using the Kolmogorov-Smirnov test while homogeneity of sample covariance matrices were tested using Box's M.

## Results

### *Fecundity and investment into the gonads*

Egg weight, fecundity, and ovary weight increased with body size. Somatic weight was better than fork length in explaining variation in egg weight ( $r_a^2 = 0.20$  vs.  $0.02$ ), fecundity ( $r_a^2 = 0.43$  vs.  $0.30$ ), and ovary weight ( $r_a^2 = 0.65$  vs.  $0.24$ ). Regressions of ovary weight on somatic weight, fecundity on somatic weight, and egg weight on somatic weight (all variables natural log transformed) were performed and their geometric mean slopes with 95% confidence intervals were: ovary weight  $\beta_1 = (0.81 < 1.36 < 1.43)$ ; fecundity  $\beta_1 = (0.81 < 1.12 < 1.43)$ ; egg weight  $\beta_1 = (0.48 < 0.70 < 0.92)$ . Ovary weight and fecundity increased linearly with somatic weight, however egg weight increased with somatic weight at a significantly decreasing rate. Ovary made up 16.2 % of the body weight and was not significantly different between years ( $t=1.13$ , d.f. = 29,  $P=0.27$ ).

Female chum salmon from Walker Creek are relatively small. A comparison of the mean postorbital-hypural length of 78 B.C. stocks (Beacham and Murray 1985b, 1987a) with Walker Creek chum salmon females (1984-1986) showed that Walker Creek females are the same size as females from small streams in their geographical region (Walker Creek: age 3  $\bar{x}=53.6$  cm, S.E.=0.44, age 4  $\bar{x}=57.1$  cm, S.E.=0.38, age 5  $\bar{x}=56.8$  cm, S.E.=1.86, east coast Vancouver Island: age 3  $\bar{x}=54.9$  cm, age 4  $\bar{x}=56.5$  cm, age 5  $\bar{x}=62.5$  cm, standard errors not reported). One Walker Creek chum salmon female had a smaller postorbital-hypural length (42.9 cm)

than did any other female out of 28 stocks in southern British Columbia observed over a 2 year period ( 1981-82, 44.1 cm, range in  $n=16 - 160$ ) as well as the 4th widest range (42%) and 3rd largest coefficient of variation (0.068) however, because the same years of ocean growth are not being compared the effect may be an environmental one.

The regression of body weight (kg) on fork length (cm) for unspawned females in 1984, 1985 and 1986, is:  $\text{weight} = 3.8 \times 10^{-6} * (\text{fork length})^{3.26}$ . The exponent confidence interval is  $2.99 < \bar{x} < 3.58$ , thus the use of Fulton's condition factor (exponent=3) is justified and although not the best fit, I will adopt here due to its widespread use, and because estimates of its heritability among salmonids are available.

Measures of body size and morphology were correlated. Adjusted snout length was positively correlated with body weight, ( $F=5.6$ ,  $r_a^2 = 0.05$ ,  $d.f=1,86$ ,  $P=0.02$ ) and condition factor ( $F=12.6$ ,  $r_a^2 = 0.12$ ,  $d.f=1,86$ ,  $P=0.0006$ ), while condition factor was positively correlated with body weight ( $F=60.7$ ,  $r_a^2 = 0.37$ ,  $d.f=1,102$ ,  $P<0.0001$ ) and fork length ( $F=7.6$ ,  $r_a^2 = 0.06$ ,  $d.f=1,102$ ,  $P=0.008$ ).

### *Growth*

A comparison of annulus widths of 1981 brood year females maturing at different ages showed that age 3 and age 4 females differed significantly in the second and third, but not in the first, year of growth (Table 1.2). Age 3 females had significantly larger annuli widths and as a result scale growth

Table 1.2:

Differences in scale increment width (mm) and instantaneous scale growth rate between females of different ages at maturity for two brood years.

## 1981 Brood year

Character	Age 3	Age 4	t	P	d.f
Increment yr 1	1.41	1.41	-0.35	0.72	69
Increment yr 2	0.91	0.75	6.84	<0.001	68
Increment yr 3	0.76	0.48	9.96	<0.001	90
Increment yr 4	N/A	0.17			
Growth rate yr 2	0.50	0.43	4.88	<0.001	90
Growth rate yr 3	0.28	0.20	8.62	<0.001	90
Growth rate yr 4	N/A	0.17			

## 1982 Brood year

Character	Age 3	Age 4	t	P	d.f
Increment yr 1	1.42	1.45	-0.49	0.63	45
Increment yr 2	0.83	0.73	2.21	0.03	45
Increment yr 3	0.60	0.60	-0.00	1.00	4
Increment yr 4	N/A	0.20			
Growth rate yr 2	0.46	0.41	2.18	0.03	45
Growth rate yr 3	0.24	0.24	-0.21	0.84	4
Growth rate yr 4	N/A	0.17			

rates during the second and third growing seasons than did age 4 females. Annulus widths of some age 3 females for the third year of growth were shrunken by resorption of scales during entry to freshwater. Resorption, however, would lessen the observed difference in width of the 3rd annulus between age 3 and age 4 females. Annuli widths and growth rate variables permitted discrimination between females maturing at different ages. The variables were correlated with the discriminant function in the following decreasing order of correlation: annulus width year 3, growth rate year 3, annulus width year 2, growth rate year 2.

Scale growth rates of mature females of different ages from the 1982 brood year were also compared. Annulus width and growth rate in the second year of growth were significantly different between ages 3 and 4, whereas there was no difference in annulus width during the first and third years of growth, although this may be a sample size problem (Table 1.2). Annuli width and growth rate variables permitted discrimination among age 3 and age 4 females. Variables were correlated with the discriminant function in the following decreasing order of correlation: increment width year 2, growth rate year 2.

#### *Relationship between age and morphology*

Age 3 and 4 females differed significantly in morphology. Age 4 females were heavier, longer, had larger snouts and fin lengths than did age 3 females (Table 1.3). A discriminant analysis of age 3 and age 4 mature chum salmon females based on morphological variables showed significant separation among ages

Table 1.3:

Differences in morphology between females of different ages.

Characteristic	Age 3	Age 4	t	d.f	P
Body weight <sup>1</sup> (kg)	3.32	4.34	7.32	162	<0.001
Fork length <sup>1</sup> (cm)	66.0	70.9	7.04	177	<0.001
POH length <sup>2</sup> (cm)	52.2	56.5	6.42	105	<0.001
Condition factor <sup>1†</sup>	1.13	1.20	3.31	162	=0.001
Snout length <sup>2</sup> (cm)	4.48	5.37	8.90	104	<0.001
Anal length <sup>2</sup> (cm)	7.34	8.03	5.91	104	<0.001
Anal depth <sup>2</sup> (cm)	5.97	7.02	4.41	104	<0.001
Caudal length <sup>2</sup> (cm)	5.69	6.46	7.16	105	<0.001
Dorsal height <sup>3</sup> (cm)	7.16	7.57	1.17	5	=0.299

<sup>1</sup> Data from 1984, 1985, 1986<sup>2</sup> Data from 1985, 1986<sup>3</sup> Data from 1986† kg cm<sup>-3</sup> x 10<sup>5</sup>



( $F=30.33$ , d.f.= 3, 92,  $P<.0001$ ) and body weight was the most highly correlated with the canonical discriminant function.

The regression of body weight on scale width was significant ( $r_a^2=0.335$ ,  $F=74.1$ , d.f.=1,144,  $P<0.0001$ ) and is as follows:

$$\text{weight} = 0.198 * (\text{scale width})^{2.62}$$

Back calculation of weights illustrates that, by delaying maturity, age 4 females increase their weight from below the mean of age 3 females of their own brood year, to above the mean of age 3 females from the following brood year. For the 1981 brood year, age 3 females returned at 3.08 kg. If age 4 females had returned at age 3, their weight would have been only 2.60 kg, by delaying maturity 1 year they returned at 3.18 kg, when competing age 3 females (1982 brood year) weighed only 2.85 kg. The situation is similar for females from the 1982 brood year when, had age 4 females returned at age 3, they would have weighed 2.90 kg and encountered age 3 females weighing 2.85 kg. However, age 4 females gained a size advantage by delaying maturity 1 year and maturing at 3.18 kg, when age 3 females (1983 brood year) weighed 2.94 kg.

The age at maturity of chum salmon females at Walker Creek was predicted using a model by Bell (1980). The fecundity of all female chum salmon arriving to spawn in Walker Creek was calculated using the fecundity on weight regression previously presented. The instantaneous rate of change of fecundity between ages ( $\log_e (\text{fecundity}_t / \text{fecundity}_{t-1})$ ) was plotted against reproductive age. The function was assumed to dome-shaped although its true shape is unknown. The age at maturity which

maximized the rate of increase ( $\log_e (\text{fecundity}_t / \text{fecundity}_{t-1})$ ) when mortality at age was included in the calculation was that age when the instantaneous mortality rate equalled the instantaneous rate of change of fecundity. The instantaneous mortality rate of adult chum salmon was taken from the literature as 0.2 (Ricker 1976). Figure 1.1 illustrates a plot of this relation and shows that the predicted age at maturity is between age 3 and age 4, assuming the dome-shaped function.

Calculation of expected fecundity from the regression of fecundity on scale width allows us to calculate the increase in fecundity between years. The fecundity on scale width regression was significant ( $r_a^2=0.291$ ,  $F=10.9$ ,  $d.f.=1,23$ ,  $P<0.003$ ) and the geometric mean regression equation is as follows:

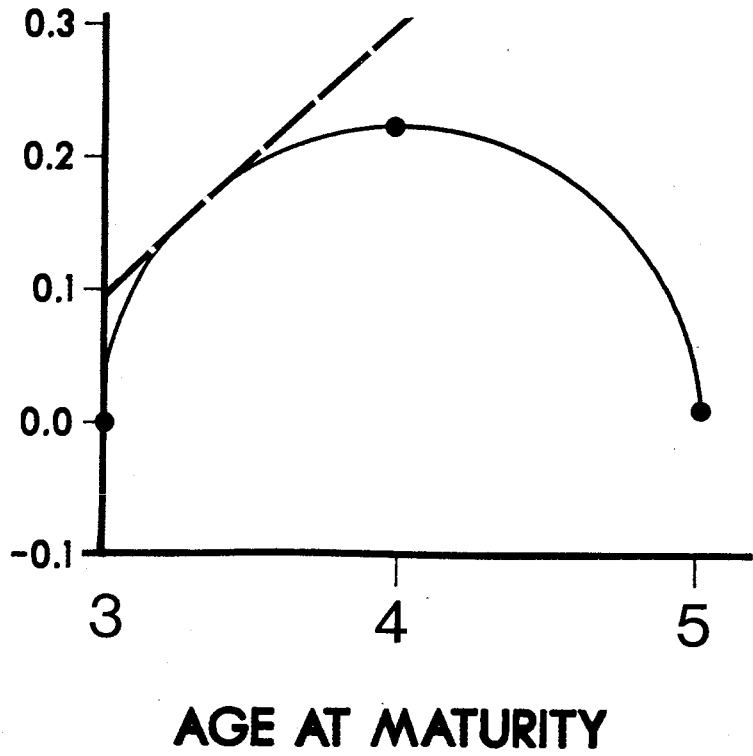
$$\text{weight} = 34.6 * (\text{scale width})^{3.38}.$$

The regression is calculated using scale widths from adults whose scales have experienced some resorption. Consequently the fecundity at previous ages will be overestimated. Adding to this effect is the possibility that the scale size of a virgin age 3 will be larger than a reproductive female of equal body size and age, since reproduction necessitates diversion of energy from growth to the gonad over and above that incurred by scale resorption. These effects reduce estimates of growth during the fourth year, and may make age 4 appear less fit than it really is. This is only of concern if the following analysis suggests that age 3 has a greater fitness.

The above notwithstanding, using back-calculated increments of growth we can compute the fecundity at age 3 of females

Figure 1.1: Age at maturity of Walker Creek female chum salmon predicted by Bell's (1980) model. Dashed line has a slope=0.2 and represents the instantaneous rate of mortality. The tangent of the two lines is the age at which the instantaneous rate of increase ( $\log_e(\text{fecundity}_t/\text{fecundity}_{t-1})$ ) equals the instantaneous rate of mortality.

**INSTANTANEOUS RATE OF CHANGE  
IN FECUNDITY BETWEEN AGES**



maturing at age 4 and hence their growth rate from age 3 to 4. The gain in fecundity is then multiplied by the annual mortality rate to yield an expected fecundity.

Calculating growth between age 3 and 4 requires that the relationship between growth within a period and size at the beginning of the period be assessed. Examining each brood year/age group separately, instantaneous growth rate between age 2 and age 3 was usually negatively correlated with scale width at age 2, but never significantly (1981 brood year, age 3;  $r=-.30$ , d.f.=24,  $P=0.14$ , age 4:  $r=-.02$ , d.f.=64,  $P=0.85$ , 1982 brood year, age 3;  $r=0.19$ , d.f.=40,  $P=0.23$ , age 4;  $r=-.12$ , d.f.=3,  $P=0.84$ ). Growth rate between age 3 and age 4 was never significantly correlated with size at age 3 (1981 brood year;  $r=-0.22$ , d.f.=63,  $P=0.08$ , 1982 brood year;  $r=-.22$ , d.f.=2,  $P=0.55$ ).

In projecting the growth from age 3 to age 4 during the 1981 brood year, I use 2 estimates. The high estimate is the observed instantaneous growth rate of age 3 females from age 2 to age 3 (0.70), while the low estimate is the observed instantaneous growth rate from age 3 to age 4 (0.17). The expected fecundity is multiplied by the inverse logarithm of two instantaneous mortality rates, rates, 0.1 and 0.3. This allows the presentation of a range of mortality around the average estimated value of 0.2 given by Ricker (1976).

Figure 1.2 illustrates the range of fecundity expected by fish at age 3 and age 4 as a function of their size at age 3,

assuming a constant growth rate and an instantaneous mortality rate independent of size. Under these conditions the functions will never intersect, but are curvilinear parallel. As we proceed along the abscissa to larger  $x$  values, the ordinate values (expected fecundity) of age 4 relative to age 3 females will not change. Therefore the fitness of maturing at age 3 compared to maturing at age 4 is independent of size at age 3. This would not be the case if growth or mortality rates between age 3 and age 4 were correlated with size at age 3.

Figure 1.2 also illustrates the observed scale size at age 3 broken down into 2 groups, females observed maturing at age 3 and at age 4. Figure 1.2 predicts fecundities of over 10000 (the predicted fecundity should a female survive would be higher since potential fecundity is discounted by mortality), whereas the maximum observed fecundity was 4150. Thus females large at age 3 could delay maturity 1 year and have a greatly increased body size and fecundity, however, they do not.

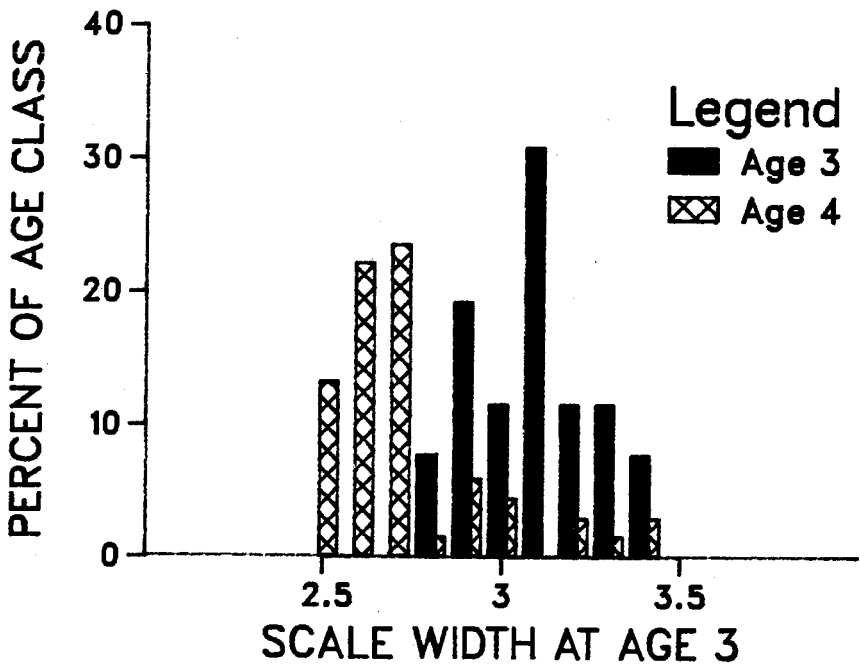
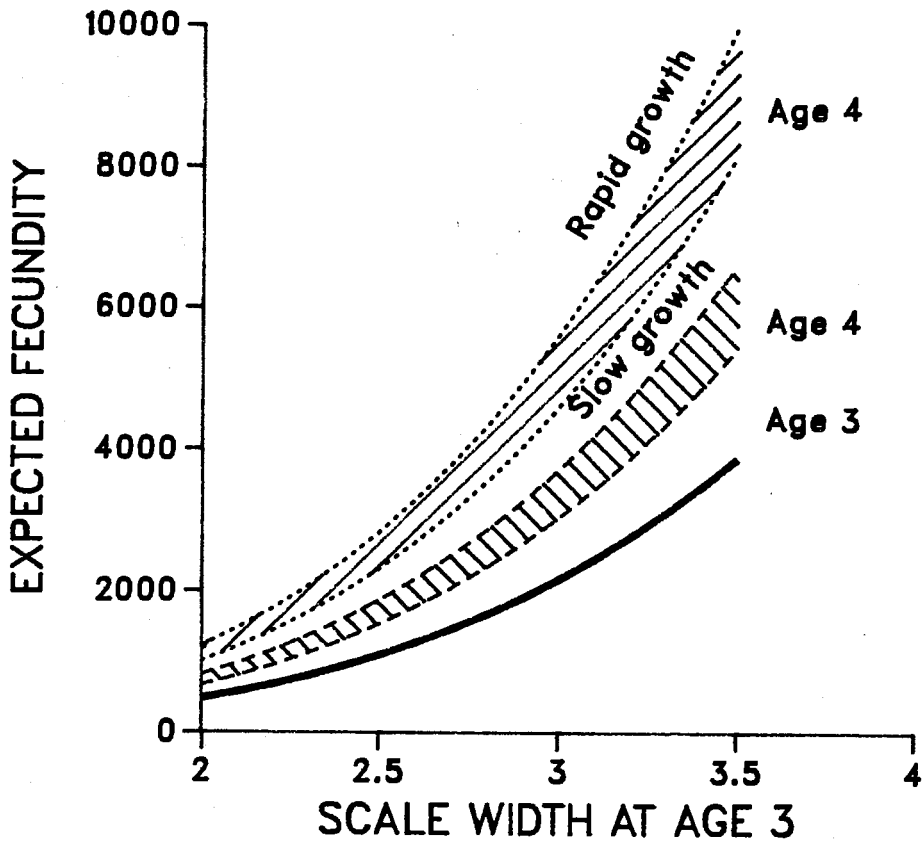
#### *Breeding competition*

Competitive interactions were broken down into categories dependent on the territorial status of the competitors. The categories were as follows:

1. between two territorial females
2. between a territorial female and a non-territorial female
3. between two non-territorial females

Only 2 interactions of type 3 were observed, and both of these interactions ended in a draw.

Figure 1.2: Expected fecundity as a function of scale width at age 3 for female chum salmon from Walker Creek, 1981 brood year. Functions at age 3 and at age 4, under rapid and slow growth, are displayed. The shaded area represents a range of instantaneous mortality from 0.1 (lower limit) to 0.3 (upper limit). The histogram illustrates the distribution of scale widths at age 3 for females that mature at age 3 and age 4.





The outcome of interactions between territorial females was determined by body size. On average the winner of a given interaction was heavier, had a longer body, snout, and higher condition factor than her competitor (Table 1.4). Arrival date, defense duration, and snout length adjusted for body length, did not differ significantly between the winner and loser of a given interaction.

The outcome of interactions between territorial and non-territorial females was determined by territorial status. In 18 observed interactions, territorial females won 16 times. The binomial probability of this occurring by chance is  $P=0.001$ . The winners of these interactions had earlier arrival dates to spawn, greater fork length, and a longer period of nest defense than did losers (Table 1.4).

To identify more clearly the importance of body morphology in distinguishing between winners and losers of territorial disputes, I compared those females that won 2 or more disputes with other territorial holders, to all other females that were observed fighting. This analysis differs from the paired contests presented earlier in that it allows a discriminant analysis of characters that may influence fighting success. In comparison to other females observed fighting ( $n=87$ ), these successful females ( $n=6$ ) had longer and heavier bodies, defended their nests for a longer period of time and had larger snouts both absolutely and relative to their body length (Table 1.5). A stepwise discriminant analysis of the 6 successful females and the other 87 females observed fighting found significant

Table 1.4:

Differences between winners and losers of competitive interactions between female chum salmon. Results of paired t-test presented.

**Territorial female vs territorial female**

Characteristic	Null Hypothesis	N	t	P
Weight	Winner $\leq$ loser	24	2.92	0.004
POH <sup>1</sup> length	Winner $\leq$ loser	20	1.91	0.032
Condition factor	Winner $\leq$ loser	17	3.12	0.004
Snout length	Winner $\leq$ loser	19	2.32	0.016

**Territorial female vs non-territorial female**

Characterisitic	Null Hypothesis	N	t	P
Fork length	Winner $\leq$ loser	17	1.89	0.039
Arrival date	Winner $\geq$ loser	17	-1.73	0.051
Defense duration	Winner $\leq$ loser	5	2.09	0.52

<sup>1</sup>POH = postorbital-hypural

Table 1.5:

Differences between females successful in competitive interactions and other competing females. A successful female is one that won 2 or more competitions with territorial females.

Characteristic	Null Hypothesis	t	P
Snout length†	Winners $\leq$ others	1.86	0.05
Snout length	Winners $\leq$ others	3.74	0.002
Fork length	Winners $\leq$ others	2.86	0.01
POH length	Winners $\leq$ others	2.60	0.01
Condition factor	Winners $\leq$ others	3.24	0.008
Defense duration	Winners $\leq$ others	2.77	0.02

† adjusted for POH (postorbital-hypural) length

differences using morphological trait variables, but only condition factor was significant in the analysis ( $F=6.77$ ,  $d.f.=1,93$ ,  $P=0.01$ ).

To summarize, the most important determinant of success in contests between females was territorial status. Females with a large fork length, early arrival date and long defense duration were more likely to be territory holders in competitions between territorial and non-territorial females. In competitions between territorial females, condition factor, body weight, snout length, and postorbital-hypural length were larger among winners in comparison to losers of contests. Condition factor discriminates successful females from other females.

Age alone was not a significant determinant of the outcome of contests, however older females tended to win more frequently, probably because of their larger body size, relative snout length, and condition factor.

The date of arrival to spawn was significantly correlated with body weight ( $r_a^2=.03$ ,  $F=4.00$ ,  $d.f.=1,97$ ,  $P=0.05$ ) but not with postorbital-hypural length ( $r=-.13$ ,  $d.f.=96$ ,  $P=.21$ ), snout length ( $r=-.19$ ,  $d.f.=96$ ,  $P=.06$ ), snout length adjusted for POH length ( $r=-.14$ ,  $d.f.=96$ ,  $P=.16$ ), condition factor ( $r=-.15$ ,  $d.f.=95$ ,  $P=.13$ ), or age (Spearman  $r=.11$ ,  $d.f.=57$ ,  $P=.201$ ). As a result, the density of female spawners encountered upon entry to the creek was not correlated with body weight ( $r=-.20$ ,  $d.f.=82$ ,  $P=0.06$ ), postorbital-hypural length ( $r=-.10$ ,  $d.f.=76$ ,  $P=0.40$ ), kype length ( $r=-0.07$ ,  $d.f.=76$ ,  $P=0.55$ ), adjusted kype length

( $r=.03$  d.f.=76,  $P=0.82$ ), condition factor ( $r=.04$ , d.f.=95,  $P=.66$ ), or age ( $r=-0.07$ , d.f.=81,  $P=.25$ ). The density of female spawners encountered in the pool where the nest was constructed was also not correlated with body weight ( $r=-.05$ , d.f.=75,  $P=0.63$ ), postorbital-hypural length ( $r=-.02$ , d.f.=69,  $P=0.89$ ), kype length ( $r=0.03$ , d.f.=69,  $P=0.79$ ), adjusted kype length ( $r=.06$ , d.f.=69,  $P=0.61$ ), condition factor ( $r=-.13$ , d.f.=73,  $P=0.27$ ), or age ( $r=0.12$ , d.f.=76,  $P=.16$ ).

The rate of nest dig-up was 4.6% (3 out of 65 nests). In all three cases of dig-up, nests completely overlapped. There was no significant difference between females that did and did not experience nest dig-up (determined by Mann Whitney U test) in body weight (d.f.=76,  $P=0.84$ ), postorbital-hypural length (d.f.=72,  $P=.71$ ), snout length (d.f.=72,  $P=.5$ ) snout length adjusted for POH length (d.f.=72,  $P=0.38$ ). The length of nest defense was not significantly correlated with body weight ( $r=.17$ , d.f.=58,  $P=.18$ ), postorbital-hypural length ( $r=.05$ , d.f.=55,  $P=.73$ ), snout length ( $r=.19$ , d.f.=55,  $P=.15$ ), snout length adjusted for POH length ( $r=.24$ , d.f.=55,  $P=.07$ ), or age (Spearman  $r=.11$ , d.f.=57,  $P=.201$ ). The length of nest defense was significantly correlated with condition factor ( $r=.25$ , d.f.=56,  $P=.05$ ), however this effect was insignificant in a multiple regression of nest defense on arrival date and water velocity at the nest site.

The length of the snout, adjusted for postorbital-hypural length, was significantly correlated with the number or percentage of eggs retained (Spearman rank correlation, number,

$r=-0.29$ ,  $d.f.=43$ ,  $P=0.028$ ; percentage,  $r=-0.28$ ,  $d.f.=41$ ,  $P=0.036$ ), however the following variables were not (Spearman rank correlation with percentage of eggs retained): body weight ( $r=.03$ ,  $d.f.=45$ ,  $P=.82$ ), postorbital-hypural length ( $r=.10$ ,  $d.f.=43$ ,  $P=.52$ ), snout length ( $r=-.05$ ,  $d.f.=43$ ,  $P=.73$ ), condition factor ( $r=-.13$ ,  $d.f.=45$ ,  $P=.40$ ), and age ( $r=.15$ ,  $d.f.=49$ ,  $P=.28$ ).

#### *Spatial pattern of stream use*

Age 4 females were more abundant in the lower parts of the creek than age 3 females in 1985 (122 vs. 182 m upstream,  $t=2.32$ ,  $d.f.=69$ ,  $P=0.025$ ). However, distance of migration was not significantly correlated with body weight ( $r=-.19$ ,  $d.f.=90$ ,  $P=.08$ ), postorbital-hypural length ( $r=-.17$ ,  $d.f.=84$ ,  $P=.13$ ), snout length ( $r=-.17$ ,  $d.f.=82$ ,  $P=.13$ ), snout length adjusted for POH length ( $r=-.02$ ,  $d.f.=82$ ,  $P=.84$ ), or condition factor ( $r=.01$ ,  $d.f.=90$ ,  $P=.90$ ). Delay in spawning (the period in days from arrival in the creek and the commencement of spawning) was significantly correlated with work performed (body weight  $\times$  distance travelled upstream from tidewater) and availability of spawning territory (unoccupied area / number of newly arrived females) in a multiple regression ( $F=6.65$ ,  $r_a^2=.17$ ,  $d.f. = 2, 54$ ,  $P=0.003$ ) ( $\text{delay} = 1.30 \times 10^{-3} \text{work} - 3.01 \times 10^{-2} \text{availability} + 1.83$ ). Work and availability were not correlated ( $r < 0.2$ ,  $d.f.=54$ ,  $P > .05$ ), even though distance travelled upstream and competition were (see Chapter 2), because of the influence of body weight in the work calculation.

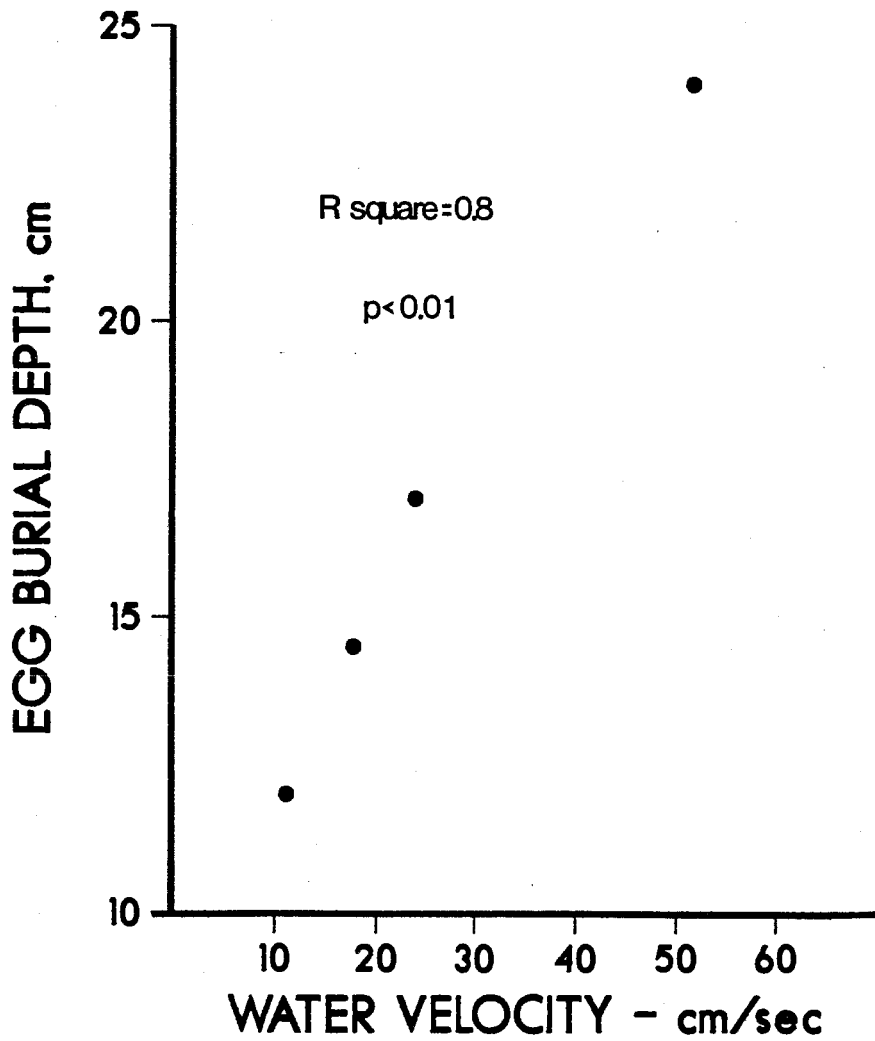
There was no significant difference in egg burial depth at know nest sites between samples taken by two independent methods; measurements from open nests at the time of spawning ( $\bar{x}=16.1$  cm) and measurements from cores of frozen substrate ( $\bar{x}=13.7$  cm) (t-test,  $t=0.92$ , d.f.=15,  $P=0.36$ ). Freeze core sampling occurred after high water discharges in January 1986 and of the 41 nest sites sampled, 21 (51%) contained no eggs, suggesting that scouring by high water discharges had removed the eggs. Consequently egg burial depth measurements from frozen substrate cores may be inaccurate. However, scour that did not remove eggs from nests likely had little effect on substrate composition, consequently substrate samples from non-scoured nests are considered accurate.

Condition factor was significantly correlated (negative) with water velocity at the nest site (Spearman rank correlation,  $r=-0.332$ , d.f.=40,  $P=0.016$ ) whereas the following variables were not (Spearman rank correlations); body weight ( $r=-.07$ , d.f.=41,  $P=.66$ ), postorbital-hypural length ( $r=.07$ , d.f.=35,  $P=.70$ ), snout length ( $r=.08$ , d.f.=35,  $P=.64$ ), snout length adjusted for postorbital-hypural length ( $r=-.07$ , d.f.=35,  $P=.70$ ), and age ( $r=.14$ , d.f.=36,  $P=.20$ ).

Water velocity at the nest site (Figure 1.3) was significantly positively correlated with egg burial depth measured prior to scouring ( $y= .287x + 9.35$ ) ( $F=15.89$ , Adjusted  $r^2=0.98$ , d.f.=1,2,  $P=0.006$ ) as was snout length adjusted for POH length (Spearman  $r=.72$ , d.f.=6,  $P=.03$ ), however, the following variables were not; (Spearman correlations) body weight ( $r=.07$ ,

Figure 1.3: Egg burial depth of female chum salmon as a function of water velocity.





d.f.=6, P=.43), postorbital-hypural length ( $r=-.03$ , d.f.=7, P=.46), snout length ( $r=.00$ , d.f.=7, P=1.0), condition factor ( $r=-.55$ , d.f.=6, P=.08), and age ( $r=-.05$ , d.f.=6, P=.45). The small multivariate sample size ( $n=4$ ) prevented a multiple regression and suggests caution in interpretation of these data since substrate size and water velocity may influence the depth of egg burial. Because measures of substrate size are available only after scouring had occurred, it is not possible to assess the relationship between egg burial depth and substrate size. It should be possible to approximate the substrate size values of those nest sites whose egg burial depth was measured prior to scouring by assigning them substrate size values of nearby nests where substrate cores were taken but where scour did not remove the eggs. However, interpolation between points of known substrate size is unjustified on account of the heterogenous nature of Walker creek substrate (fredle index:  $\bar{x}=18.78$ ,  $\sigma=13.13$ , C.V.=0.700,  $n=40$ ). The heterogeneity of Walker Creek substrate is illustrated by example at a location 170 meters upstream from tidewater where, in a distance of 1.28 meters, the fredle index changed from 8.8 to 47.6, the maximum particle size from 1879 mm to 2779 mm, and the geometric mean particle size from 21.0 mm to 74.5 mm.

#### *Egg survivorship*

Substrate samples were examined for the presence or absence of eggs. Nest sites where no eggs were found were considered to have experienced scour and thus mortality through egg removal. As previously mentioned, 51% of the nest sites sampled contained

no eggs. It is possible that the absence of eggs from a sample represents an error in measuring the nest site location, consequently 51% may overestimate the rate of mortality from scour. However, measurement errors should be random and thus no significant difference in nest site characteristics or the characteristics of females that built them is expected between true and false nest site locations. In fact, measurement error will increase variance within samples, and thus will make the detection of significant differences between samples less likely.

Females whose nests contained no eggs were significantly different in morphology from those females whose nests contained eggs (Table 1.6). Females whose nests contained no eggs had smaller relative snout lengths (Mann Whitney U test,  $Z=2.61$ ,  $d.f.=28$ ,  $P=0.009$ ) and shorter postorbital-hypural lengths (Mann Whitney U test,  $Z=2.24$ ,  $d.f.=28$ ,  $P=0.025$ ).

Nest sites that contained no eggs differed significantly in their physical characteristics from those that did (Table 1.6). Nest sites containing no eggs had lower fredle indices (Mann Whitney U test,  $Z=2.01$ ,  $d.f.=39$ ,  $P=0.045$ ) and faster water velocities (Mann Whitney U test,  $Z=1.98$ ,  $d.f.=24$ ,  $P=0.048$ ) than nests containing eggs. The higher fredle indices of non-scoured nests may be a result of female nest digging activity, which removes fine particles from the substrate (McNeil 1962).

Table 1.6:

Females that did and did not experience nest scour: differences in their morphology and nest site characteristics.

Variable	Females with scoured nests			Females with non-scoured nests		
	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n
POH length (cm)	54.9	3.03	14	57.7	3.82	16
Snout length <sup>1</sup> (cm)	4.88	0.409	14	5.31	0.408	16
Fredle index (upper) <sup>2</sup>	15.07	12.95	21	22.05	2.821	20
Fredle index (lower) <sup>3</sup>	10.09	7.591	19	16.31	10.79	21
Water velocity cm sec <sup>-1</sup>	29.40	23.10	16	15.24	23.99	10

<sup>1</sup> snout length adjusted for postorbital-hypural length

<sup>2</sup> upper strata, substrate surface to 15 cm

<sup>3</sup> lower strata, 15 cm to 30 cm below substrate surface

The intensity of natural selection on five closely correlated morphological traits was examined (Table 1.7). Selection on and for body weight, postorbital-hypural length, snout length, caudal length, and anal fin length was calculated during 5 episodes of the freshwater life history (Table 1.8). Significant selection on traits ( $s$  and  $s'$  in Table 1.8) was detected only during the growth (measured through fecundity) and nest scour episodes. Variation in fecundity resulted in the selection of increased body weight while variation in nest scour resulted in the selection of increased postorbital-hypural, snout and anal fin length. Significant selection for specific traits ( $\beta$  and  $\beta'$  in Table 1.8) was detected only during the growth and predation episodes. Growth, through fecundity, selected for increased body weight while predation selected for decreased snout, anal fin and caudal fin length. The small sample sizes made the detection of selection for traits unlikely and prevented the simultaneous analysis of the 5 traits for disruptive and stabilizing selection. Univariate analysis (each trait alone) found no significant disruptive or stabilizing selection.

Table 1.7:

Correlation matrix of morphological traits of female chum salmon (n=76).

	Weight	Pohl	Snout	Anal	Caud
Weight	1.00	-	-	-	-
Pohl	0.86	1.00	-	-	-
Snout	0.87	0.77	1.00	-	-
Anal	0.81	0.74	0.80	1.00	-
Caud	0.76	0.65	0.74	0.71	1.00

Definitions: pohl = postorbital-hypural length,  
 snout= snout length, anal = anal fin length,  
 caud = caudal fin length.

Table 1.8:

Directional selection differentials and gradients for the Walker Creek female population ( $s$ =differential,  $s'$ =standardized differential (intensity),  $\beta$ =gradient,  $\beta'$ =standardized gradient). Significance levels are of one-tail tests of Spearman rank correlations except where otherwise noted. Variance in fitness within each episode denoted as  $\sigma_w^2$ .

**Growth (fecundity) episode (1985 and 1986 data)**

Character	$s$	$s'$	$P$ †	$\beta$	$\beta'$	$P$ †
Body weight	.014	.172	.004	1.67	.560	.002
POH length	.008	.127	.275	.887	.232	.137
Snout length	.015	.112	.563	-.223	-.124	.282
Caudal fin	.006	.070	.142	-.866	-.309	.071
Anal fin	.012	.109	.394	.401	.183	.196

$\sigma_w^2 = .058$ ,  $R_a^2 = .47$ ,  $n = 28$

† significance of F statistic

**Predation episode**

Character	$s$	$s'$	$P$	$\beta$	$\beta'$	$P$
Body weight	.005	.049	.303	1.215	.386	.251
POH length	.002	.027	.338	-.169	-.039	.107
Snout length	-.001	-.007	.461	-.297	-.122	.044
Caudal fin	-.003	-.026	.278	-.551	-.201	.029
Anal fin	-.003	-.025	.249	-.548	-.205	.006

$\sigma_w^2 = .103$ ,  $R_a^2 = .13$ ,  $n = 76$

**Competition for nests episode**

Character	$s$	$s'$	$P$	$\beta$	$\beta'$	$P$
Body weight	-.008	-.083	.388	1.82	.168	.496
POH length	-.014	-.017	.204	-4.16	-.324	.143
Snout length	.001	.007	.453	1.48	.208	.418
Caudal fin	-.009	-.073	.307	-.550	-.065	.224
Anal fin	-.018	-.013	.182	-.103	-.014	.261

$\sigma_w^2 = 1.02$ ,  $R_a^2 = .02$ ,  $n = 37$

Table 1.8 cont.:

**Nest dig-up episode**

Character	s	s'	P	$\beta$	$\beta'$	P
Body weight	.000	.010	.485	.015	.006	.091
POH length	-.001	-.014	.311	.322	-.094	.447
Snout length	-.001	-.008	.410	.110	-.059	.482
Caudal fin	.001	.008	.500	.062	.030	.368
Anal fin	.001	.008	.331	.239	.117	.354

$\sigma_w^2 = .061$ ,  $R_a^2 = -.08$ ,  $n = 53$

**Nest scour episode**

Character	s	s'	P	$\beta$	$\beta'$	P
Body weight	.030	.417	.067	-3.01	-.222	.085
POH length	.025	.481	.029	2.79	.149	.232
Snout length	.068	.576	.007	3.98	.482	.085
Caudal fin	.030	.532	.007	3.97	.383	.085
Anal fin	.050	.345	.100	-2.62	-.234	.225

$\sigma_w^2 = .95$   $R_a^2 = .30$ ,  $n = 19$

**Incubation episode**

Character	s	s'	P	$\beta$	$\beta'$	P
Body weight	.006	.098	.315	1.460	.254	.202
POH length	.005	.125	.122	3.37	.384	.183
Snout length	.005	.061	.315	-.629	-.147	.213
Caudal fin	.000	.000	.437	-.146	-.030	.234
Anal fin	.004	.069	.437	-2.42	-.400	.454

$\sigma_w^2 = .12$   $R_a^2 = -.56$ ,  $n = 10$



## Discussion

### *Body size*

During the freshwater life history of female chum salmon in Walker Creek, directional selection on increased body size was detected. Large body size was advantageous as a result of its association with greater fecundity and egg survivorship from the avoidance of nest scour. The positive association between body size and fecundity as a factor influencing the fitness of body size is well known (Healey and Heard 1984, Holtby and Healey 1986, Healey 1986, van den Berghe and Gross 1987). However nest scour, while well known as a mortality agent (Wickett 1952, Neave 1953, Wickett 1962, McNeil 1962, Lister and Walker 1966 and others) has not previously been found to select larger female size (Holtby and Healey 1986).

As a result of nest scour there was actually selection of increased body, snout, and caudal fin length, while selection on body weight was insignificant. This suggests that morphology was also important during the nest scour episode. Both body morphology and size were associated with success in contests between territorial females of equal territorial status. Large, robust females were associated with low water velocity nest sites which experienced low nest scour. This suggests that larger, more robust females were able to obtain nest sites that conferred a survival advantage as a result of their superior competitive ability, a situation similar to that found among coho salmon (van den Berghe and Gross 1987).

The fitness of female salmon body size during the breeding phase of the life history is dependent on the extant levels of abiotic mortality and breeding competition. Holtby and Healey (1986) predict that large female size should be favoured when scour and breeding competition are intense, while small size should be favored when gravel quality is poor. In Walker Creek during 1985 there was high gravel porosity (quality) and deep gravel scour, yet female size was relatively small. However this apparent contradiction of prediction with observation serves to illustrate the power of measuring selection within life history episodes. A researcher testing Holtby and Healey's model in an interpopulational comparative study would be forced to conclude that the model failed to predict the observed size distribution at Walker Creek. However, in the present study, strong selection for increased female size was detected under conditions of high gravel porosity, deep scour and moderate breeding competition, as predicted by Holtby and Healey, even though the extant size of Walker Creek chum salmon females is small relative to other populations.

Conditions of high gravel porosity and deep scour are predicted to favor wide variation in female size when competition is lax and narrow variation when competition is intense (Holtby and Healey 1986). Poor gravel porosity favors less variation in female size. Competition in the present study was probably moderate, as most females spawned successfully although significant egg retention did occur. Variation in female size was wide prior to competition for nest sites in

1985, and no significant stabilizing or disruptive selection for female size occurred, thus the observed variation in female size at Walker Creek is consistent with the predictions of Holtby and Healey (1986).

In the present study, nest dig-up was infrequent and was unrelated to body size, in agreement with Schroder's (1973) findings for chum salmon at Big Beef Creek, WA., but in contrast to the situation at Deer Creek Junior WA., where the fork length of coho salmon females was negatively correlated with the frequency of nest dig-up (van den Berghe and Gross 1987). Relatively low spawner density may explain the lack of forced eviction of females from nest sites in the present study but not at Big Beef Creek where spawner densities in enclosures were greater than those found at Deer Creek Junior and yet forced eviction was rare. In Walker Creek territory owners consistently repelled intruders, suggesting that intruders did not escalate contests with territorial females. This raises the question of why territorial advantage was more important in Walker Creek than in Deer Creek Junior.

Asymmetric contests for territories between owners and intruders have been given theoretical treatment by Maynard Smith (1982). The evolutionary stable strategy (ESS) for a single contest is dependent on the relative value of a victory ( $V$ ) to the cost of the contest ( $C$ ); the contestant to whom the value of winning is greater wins. A semelparous female defending her nest from dig-up risks nothing in terms of future reproductive success compared to an intruding female who has not yet spawned

and to whom an injury could mean zero reproductive success. Thus a defending female is a "desperado" and will fight in the face of certain defeat because no other strategy has a greater fitness (Grafen 1987). Furthermore, the contest payoffs differ between owner and intruder roles. A female defending her nest after spawning stands to gain her entire fecundity by preventing nest dig-up while an intruding female gains only the difference between the fitness imparted by the contested nest site and the mean fitness imparted by the available nest sites. At Walker Creek gravel porosity was high with 83% (34 out of 41) of the nest sites having fredle indices greater than 6, a porosity that would result in over 80% survival to coho salmon eggs (Lotspeich and Everest 1981). Gravel porosity at Deer Creek Junior was low as only 18% (36 m<sup>2</sup> out of 205 m<sup>2</sup>) of the usable spawning area had a fredle index greater than 6. The eggs of chum salmon are usually larger than those of coho salmon (Fleming et al. 1987, this study Chapter 3) and consequently their survival in a given size of gravel may be lower than that of coho salmon. However, this difference is unlikely to be great enough to compensate for the large difference in mean porosity between Walker Creek and Deer Cr. Junior. At Big Beef Creek gravel porosity was high as the experimental channels were filled with coarse gravel that contained no sand (Schroder 1973). If there is little difference in the relative fitness value of territories, intruding females are unlikely to risk injury in a contest for territories, thus the observed contrast in contest escalation behavior of Deer Cr. Junior with Walker and Big Beef Creeks is consistent with the observed differences in nest site porosity.

Female salmon competing for nest sites face an additional asymmetry beyond ownership, that of body size. Relatively large contestants are more likely to escalate contests for territories because their chance of injury is lower and their chance of winning higher. The coefficient of variation in female body size (fork length) at Deer Creek Junior (0.14) is not significantly greater than that at Walker (0.07) or Big Beef (0.06) creeks, thus greater variation in body size alone cannot explain the higher incidence of nest site eviction at Deer Creek Junior. Among male fiddler crabs (Uca pugilator) contests for burrows are decided by ownership, however, sufficiently large size differences can override this effect (Hyatt and Salmon 1978). In contests between funnel-web spiders (Agelenopsis aperta), outcomes are decided by a combination of ownership, territory value and the relative size of contestants (Reichart 1978).

Female size was not correlated with egg burial depth at Walker Creek and this may be due to my inability to control for substrate size effects, however, where substrate size is large, like at Walker Creek, the influence of female size on egg burial depth may be minimal. van den Berghe and Gross (1984) found selection for increased body size, partly because the greater egg burial depth of large coho salmon females reduced the frequency of nest dig-up. Holtby and Healey (1986) found that the effect of coho salmon female size on egg burial depth did not explain interannual variations in egg mortality at Carnation Creek. Ottaway et al. (1981) found a positive correlation between female size and egg burial depth among brown trout

(Salmo trutta). Elliot (1984) found no relationship between female size and egg burial depth among brown trout in 2 English streams, and suggested that burial depth differed between the 2 streams primarily as a result of substrate size.

Increases in female size may not always result in significantly greater egg burial depth and subsequently increased egg survival. Large particles may determine the maximum egg burial depth, hence in large substrate the influence of female size on egg burial depth may be small. Substrate is compact prior to nest construction, is loosened by the first female using a spawning site and replaced with finer, less compact material. This may make a previously occupied nest easier to dig-up than virgin substrate, consequently small females may be able to dig-up the nests of larger females. Furthermore, mechanical shock from digging may not displace the eggs but may still kill them, since eggs are sensitive to vibration until the eyed stage (Smirnov 1955) and sensitive to shock until epiboly (Jensen and Alderdice 1983). Thus large females may bury their eggs more deeply, but this will not always result in a significantly reduced mortality from nest dig-up or scour.

The length of the nest defense period is important to egg survivorship because undefended nests are vulnerable to dig-up by other females (McNeil 1964, van den Berghe and Gross 1984). In the present study, body size played no role in determining the length of the nest defense period: this agrees with studies of female chum salmon at Big Beef Creek (Schroder 1973), but

disagrees with studies of female coho salmon at Deer Creek Junior where there was a significant positive correlation between female size and freshwater lifespan.

Large females are expected to have a longer freshwater lifespan but not because they have a slower metabolic rate. Metabolic rate does not vary with size among sockeye salmon from 0 to 10°C (Brett and Glass 1973). There is no evidence that large females have a proportionally greater store of fat than do smaller females. However, if a given tail beat-frequency requires a particular metabolic rate, and if the relationship between tail-beat frequency and speed is size dependent, then longer females will swim faster at a given metabolic rate (Brett and Glass 1973). As a consequence large females expend less energy per kilogram to swim a given distance than do small females. We would thus expect large females to consume their energy reserves less quickly than small females. This would not be the case in Walker Creek in 1985 because shallow water depths made migration difficult for large females. Furthermore, because feeding ceases just prior to freshwater entry, the effect of body size on freshwater lifespan may be most detectable after long freshwater migrations. Spawning grounds on Walker and Big Beef creeks are located within 1 km of tidewater whereas they are 50 km upstream from tidewater on Deer Creek Junior, and this may be a cause of the difference between the creeks in the relationship between female size and freshwater lifespan.

Among Deer Creek Junior female coho salmon, fork length was positively correlated with nest site porosity which in turn was

positively correlated with egg survival (van den Berghe and Gross 1987). This was not the case in the present study, probably because ownership was more important than size in determining the outcome of contests for territories. Female size was unrelated to egg survival during incubation, possibly because the relatively high porosity of Walker Creek substrate or because the critical period, that prior to hatching when oxygen deprivation has the greatest effect on egg survival, was not examined in this study.

Egg retention was predicted to be negatively correlated with female size as a result of their greater competitive ability. The lack of correlation between egg retention and female size may be a result of the delay in migration experienced by larger females. However, size had no effect on egg retention at Big Beef Creek where low flow conditions were absent, again suggesting that size was a minor factor in determining who obtained nest sites in Walker and Big Beef Creeks.

### *Morphology*

Significant selection of increased snout and caudal fin length by nest scour was detected in this study. Selection for these traits was not significant and this could be a result of the small sample size, as multivariate selection analysis with small samples tends to underestimate selection when it is weak (Endler 1986). The selection gradients during the nest scour episode indicated positive selection for snout and caudal fin length and negative selection for body weight. This suggests



that nest scour actually selected for a robust morphology, not just large body size. Females with robust morphologies (high condition factor) occupied low water velocity nest sites and these nest sites experienced low rates of scour. However, large body size and body robustness are correlated and both contribute to success in competitions for nest sites. Whether body size or morphology or both will be selected for will depend on their heritabilities, which I will discuss shortly.

Relatively large snouts were advantageous in competition for nest sites but significant selection was not detected during the episode of competition for nest sites. This seems counter-intuitive as relative snout size was significantly negatively correlated with egg retention. This must be a result of the lesser sample size in the multivariate analysis, as relative snout size was significantly negatively correlated with egg retention. The predation episode selected for smaller anal and caudal fin size but significant selection on these characters was not detected, thus selection for less robust morphology is implied. These results suggest that robust morphologies suffer greater predation, possibly because their swimming performance in shallow water is poor.

#### *Age at maturity*

Bell's (1980) demographic life history model model predicted age 3.3 as the 'optimal' age. Bell's model shows that maturity will be deferred so long as increases in the intrinsic rate of increase due to increased fecundity offset the mortality rate.

Bell's life history model is unsatisfactory in several respects. It assumes density independence, while mortality is likely density dependent during the marine (Beacham and Starr 1982, Peterman 1982) and freshwater (Hunter 1959, McNeil 1964 and others) life stages. Furthermore, it is not possible for females to mature at any age, as implied by the continuous curve between ages 3 to 5. For example, returning to spawn at age 3.7 would mean spawning during August when Walker Creek has no flow and when reproductive success would be zero. Consequently one needs to consider maturity at 3 or 4 as discrete alternatives, as I have done here. While Bell's model does have value as an heuristic tool, it is probable that its assumptions are violated.

Healey (1986) tested the hypothesis that Pacific salmon mature at an age that maximizes  $r$ , the instantaneous rate of growth, in the Euler equation. His results for chum salmon show that  $r$  is maximized between ages 3 or 4, which agrees well with the commonly observed ages of chum salmon in the literature (Beacham 1984b, Beacham and Murray 1985b) and in the present study.

Although in the present study those female chum salmon that grew most rapidly matured at a younger age, as was found by Helle (1975), future growth was not significantly negatively correlated with size at age 3. Consequently the hypothesis that age at maturity is a conditional ESS cannot be corroborated unless a negative correlation between mortality rates and size at age 3 is assumed. If relative growth or mortality were

negatively density-dependent, then age at maturity could be a conditional ESS or 'best of a bad situation' strategy (cf. Gross 1984) where females large at age 3 mature at age 3, since delaying maturity would result in a lower expected fecundity.

Equal fitness and frequency-dependence are conditions of the mixed ESS, an alternative explanation for the observed pattern of age at maturity among female chum salmon. Female salmon might exhibit different foraging behaviors in the ocean, risk-prone or risk-averse, and growth might be positively correlated with the mortality associated with these behaviors. The association of high mortality with fast growth and low mortality with slow growth would tend to equalize the fitness of different ages of reproduction. Frequency dependence would result because the payoff to the risk-prone strategy would depend on foraging success which, in turn, would be related to the density of competitors.

### *Conclusion*

Some of the findings in this study suggest that selection for larger body size, greater age, and more strongly developed morphology should be occurring. However, even if a trait is selected for, a response to selection may not occur if pleiotropic effects are antagonistic, if the trait is of low heritability, or if selection during other phases of the life history occurs in the opposite direction. If two traits are both under selection by the same agent but have different heritabilities, one trait may respond while the other does not.

For example, if morphology was more heritable than body size at maturity, we expect a response from morphology while body size would remain relatively unchanged. Whether age at maturity and growth are heritable among female chum salmon is unknown, although differences between populations in mean age and body size at maturity (Beacham and Murray 1987a) suggests they are, as does evidence among other species of Pacific salmon that age and growth are heritable (Donaldson and Menasveta 1961, Ricker 1972, 1981). For example, heritability of body size among pink salmon is 0.22 to 0.30 (Ricker 1981). Among Atlantic salmon the heritability of body weight and length may be greater than that of condition factor (dam heritabilities: weight  $h^2=0.15$ , length  $h^2=0.18$ , condition factor  $h^2=0.05$ , Gunnes and Gjedrem 1978) while other studies have shown condition factor to be highly heritable ( $h^2=0.04$  to  $0.81$ ) (Naevdel et al. 1976). Among rainbow trout (Salmo gairdneri) the heritability of condition factor ( $h^2=.46$  to  $.66$ ) is greater than that of body length and weight ( $h^2=.13$  to  $.38$ ) (McKay et al. 1986). The dam heritability of age at maturity ranges from 0.49 in Atlantic salmon to 0.26 in rainbow trout (Gjerde and Gjedrem 1984). The heritability of age at maturity among chinook salmon is estimated to be 0.24 (Smoker 1984) and 0.25 (geometric mean, Ricker 1981).

Even if a response to selection occurred, the future trend in body size cannot be predicted since selection as detected here may occur infrequently. For example, the mortality effects of scour are to some degree density-dependent, since scour-free nest sites are likely limited in number, and a combination of

deep scour and intense female competition may be necessary to select for large female size.

If growth and morphological trait size are heritable in chum salmon, and if the measured gradients of selection are close to the true gradients, an evolutionary response of increased female body size, age at maturity, condition factor, and snout development are predicted. Selection on body size, morphology, and age in other episodes of the life history must be considered when predicting the evolutionary response. Mean size of chum salmon in southern British Columbia declined by 0.5 kg from 1951 to 1975 while age increased by 0.37 yr (Ricker 1981). Whether trends in size and age are a result of commercial fishing or environmental fluctuations is unknown, however the intensity of size selection by gill-net fisheries for chum salmon has been weak (Ricker 1981) and the effect of size selection is not easily predicted (Healey 1986). Furthermore, the extrapolation of selection intensities from one population to another or between years in order to explain extant or future trait distributions is not recommended (Endler 1986).

On average, delaying maturity appeared to increase weight from below to above that of the competing age class encountered during spawning, suggesting that small body size was disadvantageous. If mortality rate and growth rate are not correlated with size at the beginning of a growth period, females maturing at age 3 could make large gains in fecundity by deferring maturity until age 4. That the large potential gain in fecundity is not being made suggests that being very large may

have some cost.

## CHAPTER II

# THE EFFECT OF BREEDING COMPETITION AND ABIOTIC FACTORS ON THE BEHAVIOR OF FEMALE CHUM SALMON

### Introduction

Evolutionary theory predicts that behavior and morphology should be molded by natural selection into adaptations that enhance lifetime reproductive success. Previous studies have illustrated that female competition for spawning sites can generate intense natural selection in the morphology of female Pacific salmon (van den Berghe and Gross 1987). Moreover, in an interpopulational comparative study, Fleming and Gross (1987a) showed that mean long-term spawner density is correlated with the degree of development of several morphological features advantageous in competitive interactions. Thus, the development of morphology and life histories within populations as well as its variation among populations can be explained by female competition. However variation in breeding behavior within salmon populations also exists. If female competition causes significant natural selection, behavior should exhibit responses to competition. The purpose of the present study was to investigate whether female competition can explain variation in breeding behavior within a population. Specifically, I examined the response of breeding behavior to variation in the intensity of breeding competition among female chum salmon.

Female competition is predicted to influence female behavior and thus should determine the pattern of breeding habitat selection. Egg survival is positively correlated with the porosity of the incubating substrate (Lotspeich and Everest 1981), and females show a preference for high porosity substrate (van den Berghe and Gross 1987). The porosity of utilized nest sites should decrease as female competition increases because a larger proportion of the population will be forced into the less desirable, low porosity nest sites.

Body morphology and size influence competitive ability and hence reproductive success as discussed in Chapter 1. A correlation between body size and behavior could confound the relationship being examined here, that between mortality from breeding competition and behavior, consequently the relationship between body size and behavior will be examined.

The reproductive success of female salmon is strongly affected by competition for nest sites. High female spawner densities inhibit nest construction and as a consequence females retain eggs in their bodies after death (Schroder 1981). Nest dig-up can be a major source of egg mortality (McNeil 1962 & 1964a, van den Berghe and Gross 1984, Hayes 1987). Females evicted from their nests or who leave their nests undefended risk nest dig-up by newly arriving females. As a result strong natural selection exists for competitively advantageous traits (van den Berghe and Gross 1987). One of these traits is nest defense, which reduces egg mortality by preventing destructive re-use of nests by competing females.



Chum salmon are semelparous and do not feed after entering fresh water to spawn; consequently their energy reserves are limited. Any factor that increases the rate of energy expenditure will decrease the freshwater lifespan and possibly the period of nest defense. Abiotic factors known to effect the period of nest defense and measurable in this study are water temperature and water velocity (van den Berghe and Gross 1986). Biotic variables could, in theory, also affect variation in the period of nest defense. High spawner densities result in more frequent competitive interactions among females (Schroder 1981) which in turn increases the rate of energy consumption (Brett 1970). Intuitively the duration of nest defense should be negatively correlated with date of arrival to spawn, since early arriving females are at a greater risk of nest dig-up. However, water temperature, water velocity and measures of female activity may confound this relationship as they are known to be negatively correlated with residence time among coho salmon (van den Berghe and Gross 1986).

The timing of breeding also should be molded by natural selection. If mortality of eggs from female breeding competition varies in time, it could play an important role in the evolution of arrival date to spawn. In addition, abiotic factors, instream predation, and fishing mortality might shape the distribution of arrival date to spawn. As a result, traits beneficial in competition and adaptations to the abiotic environment might show temporal patterning in their intensity of expression.

## Methods

Field studies were conducted as described in chapter 1, except for the following.

The total spawning area was determined by summing the wetted area greater than 10cm deep in those pools used by spawning chum salmon females. The area defended per territorial female was not measured for each individual but was determined within each pool as the total wetted area greater than 10 cm deep divided by the number of territorial females present.

The number of males attending a female and the number courting her (as defined by Schroder 1973) was recorded. Attending males were easily recognized because they formed a cluster directly downstream of the female and fought with the dominant (alpha) male during the courting process.

## Results

In 1985 134 female chum salmon arrived to spawn at Walker Creek. Of these, 14 (10.4%) were retained at the fence for fecundity measurement and 3 escaped downstream. The 117 remaining females were tagged and released upstream of the fence to spawn; of these, 55% (65) were observed constructing and defending nest sites, 18% (21) were observed holding over and defending redds, 9% (11) were seen in a centralized location but without an apparent nest site, 11% (13) females were observed in the creek but never in centralized locations and 6% (7) were never seen after release above the fence. Seven of the 117 females were partially spent and further 7 completely spent. These females were less likely to be observed constructing or defending nests. While 83.4% (86 out of 103) of the fresh or ripe females were observed constructing or defending nests, only 29 % (4 out of 14) of the partially spent or spent females were observed doing so. No spent females were observed constructing a nest, although 2 spent females were observed defending a territory where no nest was present.

Eighty-five females were recovered after death and 3 of these died by predation: the suspected predator is the river otter, Lutra canadensis. Uncoagulated blood and non-waterhardened eggs indicated that dead fish were killed by predators and were not simply eaten after dying. Instream predation rate prior to spawning is estimated at 3.5 % (3 out of 85). Humans were also observed catching chum salmon and the

predation rate is 8.5% (10 out of 117) if females that disappeared after release above the fence are considered to have suffered predation and are included in the estimate.

The mean fecundity of Walker Creek females was 2421 ( $\sigma=827$ ,  $n=14$ ). For the purposes of estimating proportional egg retention, the fecundity of spent females was estimated using the fecundity versus fork length regression (fecundity =  $5.521 \times 10^{-6}$  fork length<sup>4.69</sup>,  $F=27.8$ ,  $r_a^2=0.674$ ,  $P=0.0002$ , d.f. = 1, 12). While body weight explained more of the variation in fecundity, using fork length as the independent variable provided a 25% larger sample size. Egg retention was a significant source of egg mortality. After death, 50 females were collected and sampled for egg retention. Twenty-nine females (58%) retained no eggs, 8 females (16%) retained less than 10 eggs, while 13 females (26%) retained over 10 eggs. The arithmetic mean egg retention was 201 eggs; this represented 7.8% of the calculated mean individual fecundity of this group (2566 eggs).

Most females constructed their own nests in close proximity in a structure called a 'redd'. However, 16 of the 65 females (24.6%) constructed nests in a second location physically removed from the first by 2 or more meters. Of these 16 females, only 5 were observed to build their nests more than 5 meters apart such that defense of both nest sites did not occur. The second nest was usually located upstream of the first (4 out of 5 times). Females that built nests 5 or more meters apart experienced a higher female density during the first five days

of stream residence (.20 vs. .12 m<sup>-2</sup>) (Mann Whitney U test, Z=2.07, d.f.=11, P=0.04), arrived with a larger pulse of females (9.6 vs. 3.9 females) (Mann Whitney U test, Z=2.71, d.f.=11, P=0.007) and retained more eggs (117 vs. 0 eggs) (Mann Whitney U test, Z=2.23, d.f.=4, P=0.03) than did those females that built their nests closer together than 5 meters, but there was no difference between these groups in adjusted snout length (n=12), fork length (n=16), body weight (n=16), or arrival date to spawn (n=16).

#### *Redd site location*

The spatial pattern of nest site location was dependent upon the spatial scale within which it is examined. Within the entire stream, nest sites were aggregated. Within aggregations, however, female distribution was more uniform. Only areas of the stream with water depths greater than 12.5 cm and with a surface area greater than 21 m<sup>2</sup> (average 69.6 m<sup>2</sup>,  $\sigma=37.7$ , n=86) were used by female chum salmon for spawning. All spawning areas included a large area of cover, either an undercut bank or wood debris. These physical areas were easily recognizable and are commonly defined in the literature as 'pools' (Hoopes 1972).

Of the 620 m of available stream, females occupied only the lower 460 m where the spawning area used was 246 m<sup>2</sup>. The stream discharge during the study was 0.034 m<sup>3</sup>sec<sup>-1</sup> which was low enough to cause the stranding of females migrating between pools. As a result, upstream spawning areas were more difficult

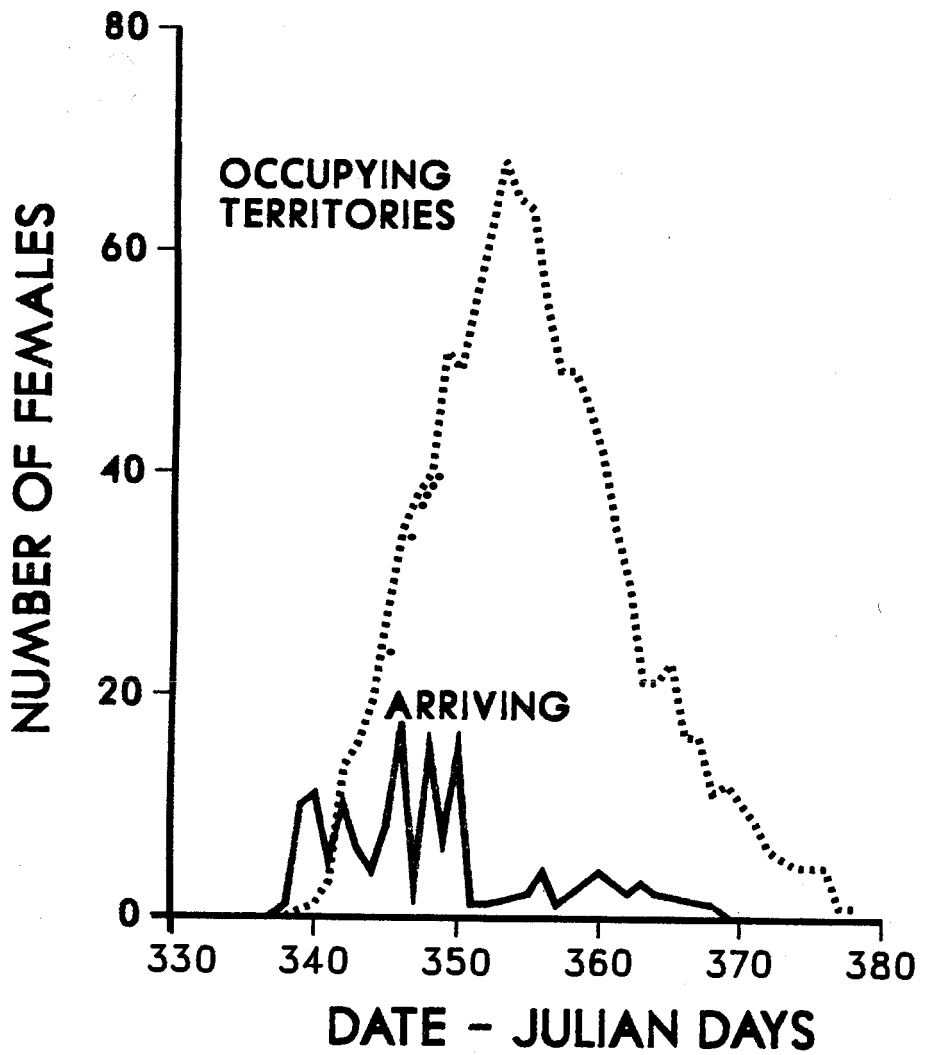
to reach, and fewer females utilized the upstream areas.

### *Intensity of competition*

The intensity of competition for nest sites varied with time (Figure 2.1). Females first arrived in the creek on December 4 (julian day 338) 1985. Arrival thereafter was not uniform but occurred in pulses over a 30-day period. The size of daily immigration (referred to as the female pulse size) reached a maximum of 17 females on December 12 (day 346). The last immigration occurred on January 3 1986 (day 368). The density of female chum salmon in the creek increased from December 4 (day 338) to a peak of 64 territorial females present on December 16 (day 350). At this time the overall density (number females/spawning area occupied) of female chum salmon defending territories was  $0.26 \text{ m}^{-2}$ . Within individual pools the spawner density was greater (.57, .55, .35, .43, .56;  $\text{m}^{-2}$ ) than the overall density, while outside of pools some females had entire riffles to themselves (density =  $.02 \text{ m}^{-2}$ ). The actual area defended by each female was not determined, however, within pools females invariably fought with neighbouring territorial females as a result of high spawner densities. Consequently I calculate territory size within pools as the inverse of female spawner density ( $\bar{x} = 2.0 \text{ m}^2 \text{ female}^{-1} \text{ n}=5$ ).

After peaking, density declined until it reached zero by January 10 (day 375), 1986. As a consequence of intrapopulation variation in arrival date, female salmon encountered a spawner density and female pulse size specific to the date of arrival to

Figure 2.1: Temporal pattern of territory occupation and arrival to spawn by female chum salmon in 1985.





spawn.

### *Female behavior*

Female chum salmon responded to increasing female density by migrating further upstream into unoccupied areas (Spearman rank correlation = 0.40,  $P < 0.001$ ) (Figure 2.2). Once early arriving females began to die, the female density in the lower reaches of the stream declined and late arriving females occupied the lower reaches, maintaining the gradient of decreasing spawner density with increasing distance from tidewater ( $r_a^2 = 0.63$ , d.f.=1,8,  $P=0.0007$ ) (Figure 2.3).

Female chum salmon arriving during periods of high female density retained a higher percentage of eggs than did females arriving to spawn at low female densities. This is shown by dividing the population of females into two groups, those that arrived when female density ranged from zero to one half maximum (0 to  $.13 \text{ m}^{-2}$ ) and those that arrived when female density was one half maximum to maximum ( $.13$  to  $.26 \text{ m}^{-2}$ ). I then compared egg retention and found the low density group retained 115 eggs per female while the high density group retained 330 eggs per female (Mann-Whitney U test,  $Z=2.65$ , d.f.=48,  $P=0.008$ ). Egg retention was negatively correlated with relative snout size, but not with other measures of morphology or size (Chapter 1).

Male spawning activity was not associated with female egg retention. On several occasions females crouching in the nest in preparation to release eggs were displaced from the nest by the

Figure 2.2: Distance of migration upstream from tidewater as a function of density of female chum salmon spawners in entire stream.

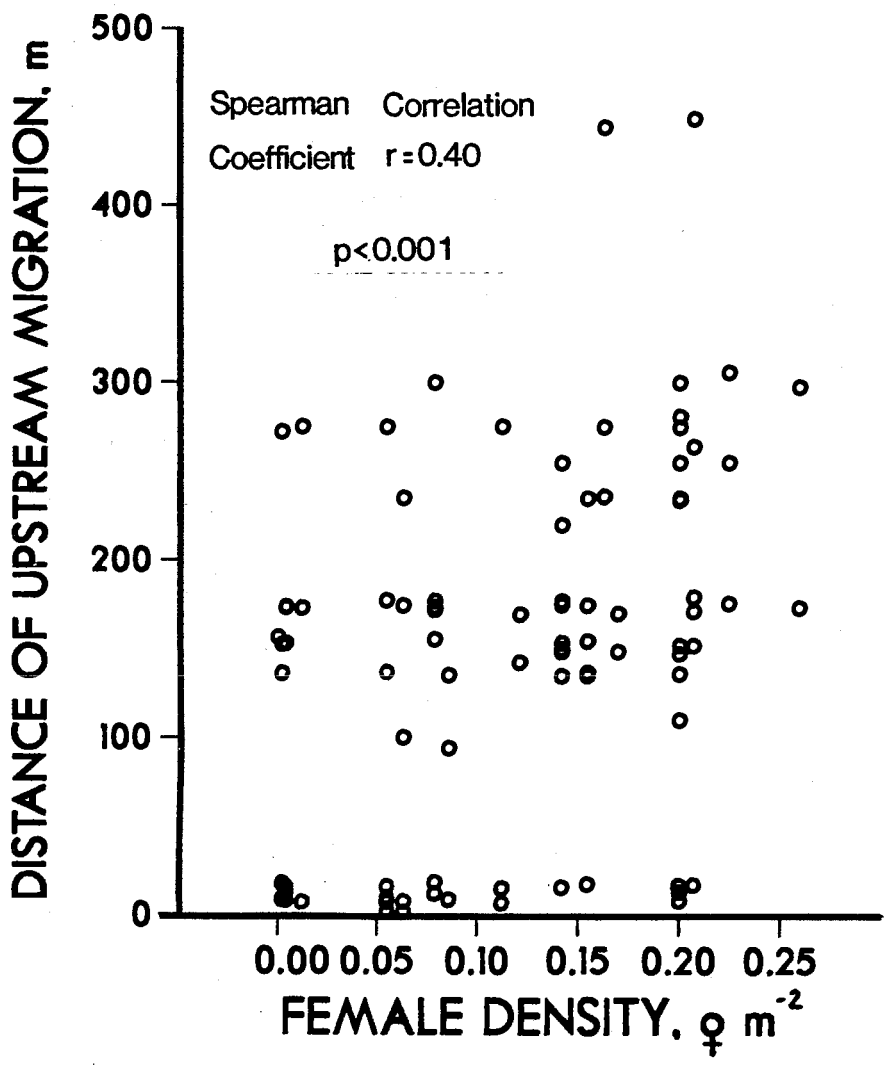
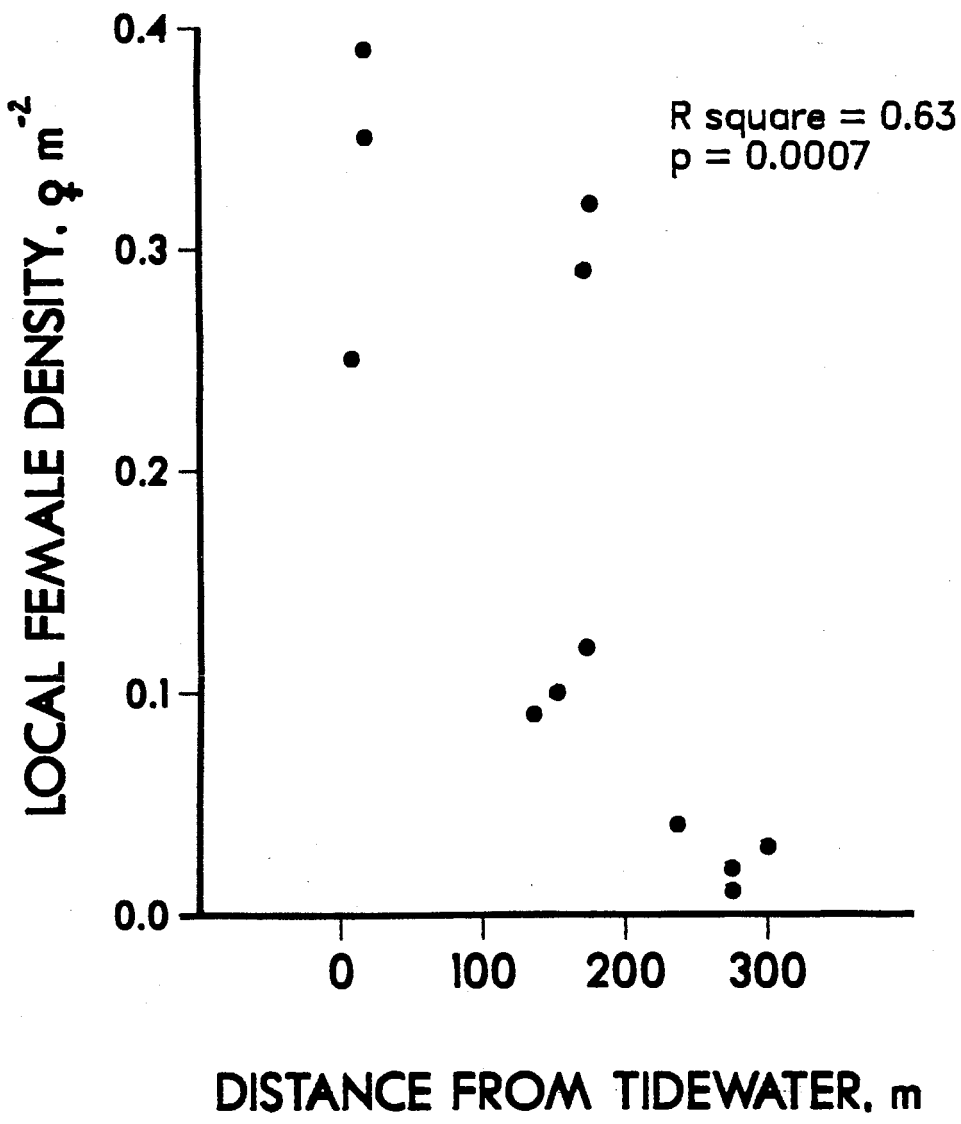


Figure 2.3: Local density (within pool) of spawning chum salmon females versus pool distance upstream from tidewater.



movements of satellite males attempting to participate in the spawning. This interrupted female spawning. However, females that spawned with male groups having more members than average ( $\bar{x}=1.47$ ) did not retain significantly more eggs than females that spawned with male groups having fewer members than average (Mann-Whitney U test,  $Z=-1.54$ , d.f.=35,  $P>0.05$ ).

To test whether water temperature had an effect on egg retention, I used the variable of mean temperature experienced during the first five days of the freshwater lifespan (the maximum period females delayed prior to spawning). I used the mean of this temperature variable ( $2.5^{\circ}\text{C}$ ) to divide the population into two groups and found that females experiencing temperatures greater than the mean did not retain more eggs than females experiencing temperatures below the mean ( $n=50$ ).

Substrate was not significantly layered at Walker Creek. There was no difference in porosity between the upper strata (0 to 15 cm deep) and lower strata (15 to 30 cm deep) ( $n=41$ ). The upper and lower substrate layer of nests escaping scour were not significantly correlated ( $n=12$ ). Measures of nest site porosity reported here are from the upper strata except where otherwise mentioned.

Female density influenced the quality of nest site obtained. Gravel porosity at the nest site was not significantly correlated with female density in the entire stream but with local female density (within pool) at the time of nest construction ( $r_a^2=.29$ ,  $F=6.11$ ,  $P(1\text{-tail})=0.02$ , d.f.=1,11)

(Figure 2.4). Females arriving at the stream with only a small number of other females (female arrival pulse size) obtained territories of greater porosity than females arriving with many other females ( $r_a^2=.15$ ,  $F=3.28$ ,  $P(1\text{-tail})=0.045$ ,  $d.f.=1,12$ ) (Figure 2.5). However, females that built their nests further upstream from tidewater obtained nest sites of greater porosity ( $r_a^2=.31$ ,  $F=6.88$ ,  $P(2\text{-tail})=0.02$ ,  $d.f.=1,12$ ) (Figure 2.6).

An alternate explanation for the results is that a linear gradient of porosity with distance upstream from tidewater existed, resulting in a spurious correlation of density and porosity. However, there was no significant positive correlation of distance upstream with porosity in the lower strata ( $r=.04$ ,  $n=21$ ,  $P(1\text{-tail})=0.43$ ), with porosity in the lower strata of coho salmon nests ( $r=.34$ ,  $d.f.=6$ ,  $P(1\text{-tail})=0.17$ ), or with porosity in the upper strata of coho salmon nests ( $r=.32$ ,  $d.f.=8$ ,  $P(1\text{-tail})=0.22$ ). These results suggest no linear gradient of porosity with distance upstream from tidewater.

In every case where stream and intra-gravel water at chum salmon nest sites differed in dissolved oxygen and temperature, temperature was higher and dissolved oxygen was lower in the intra-gravel water than in the stream water (Figure 2.7). Surface water temperature increased significantly with time over the four month incubation period while the intra-gravel water temperature changed negligibly. Dissolved oxygen was constant over time in the intra-gravel water, although it was much less than in stream water (Figure 2.7).

Figure 2.4: Fredle index (porosity of gravel) at the nest site of individual female chum salmon as a function of the local female density (within pool) they experienced.



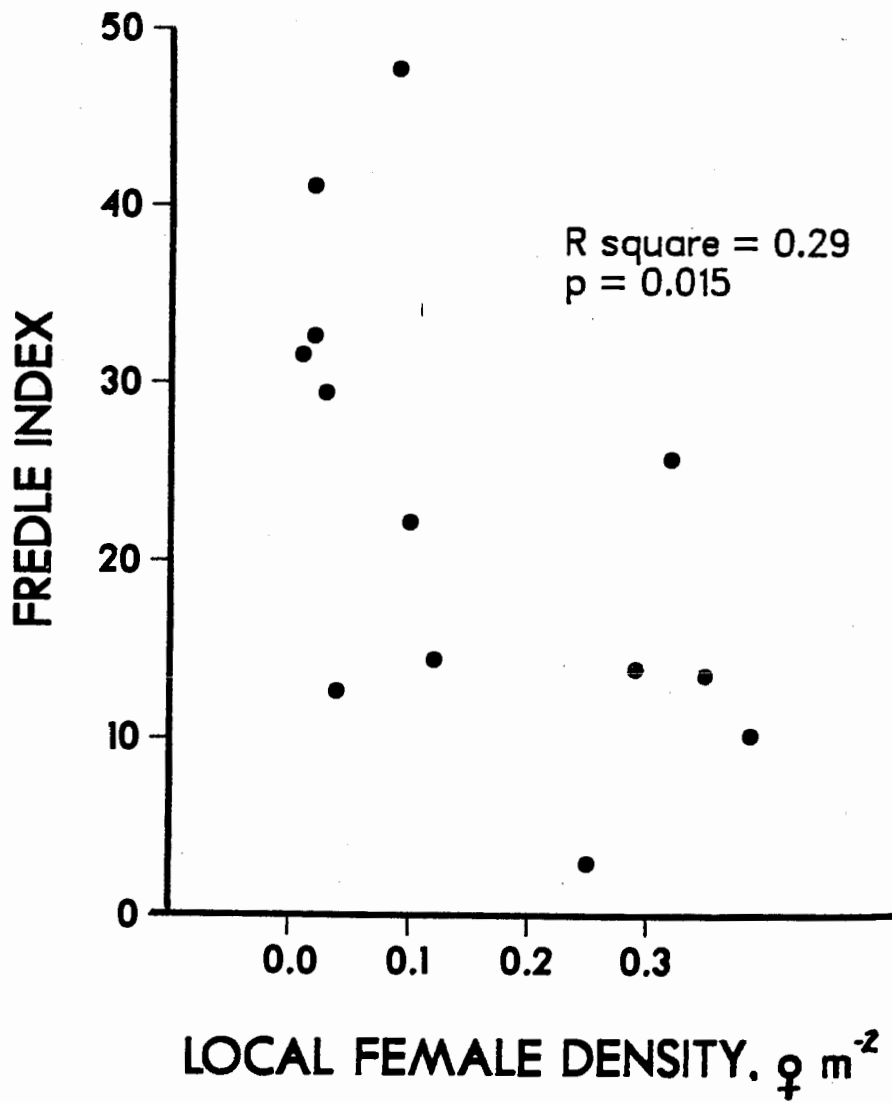


Figure 2.5: Fredle index (porosity of gravel) at the nest site of individual female chum salmon as a function of the female arrival pulse size they experienced.

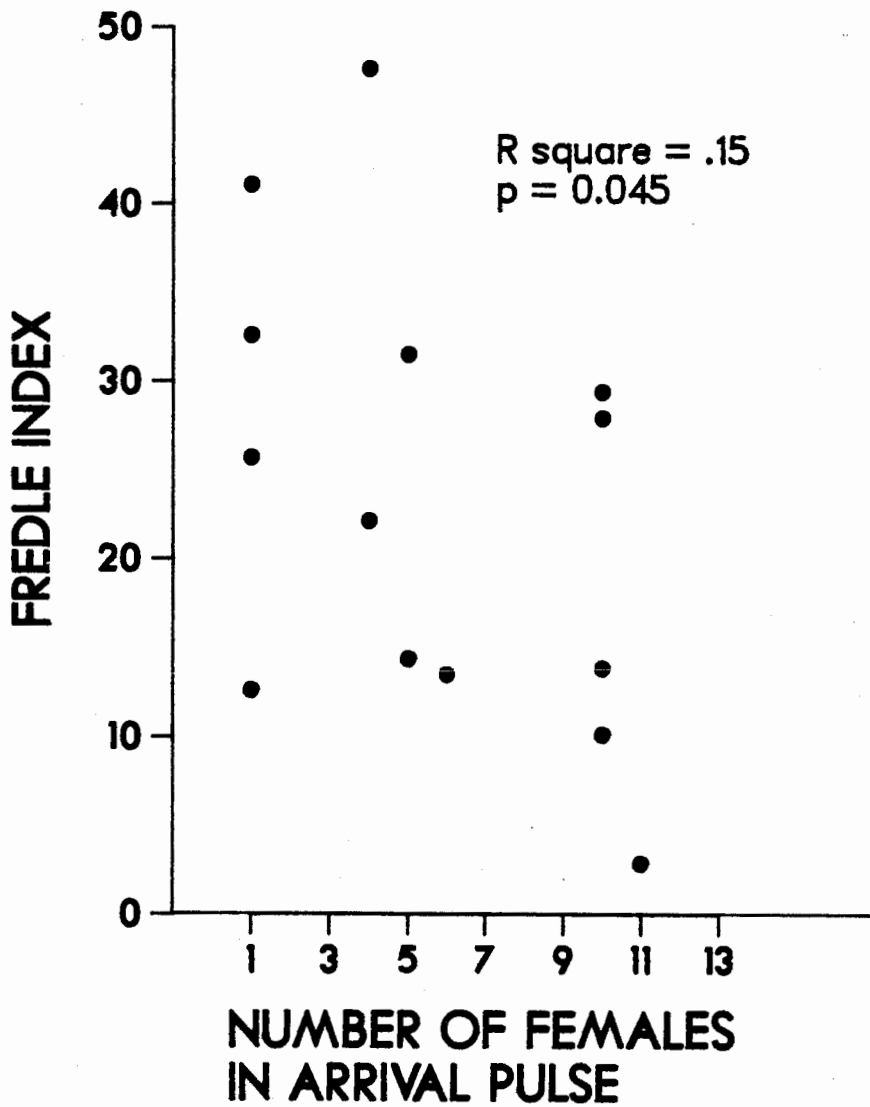


Figure 2.6: Fredle index (porosity of gravel) at the nest site of individual female chum salmon as a function of the distance of the nest site upsteam from tidewater.

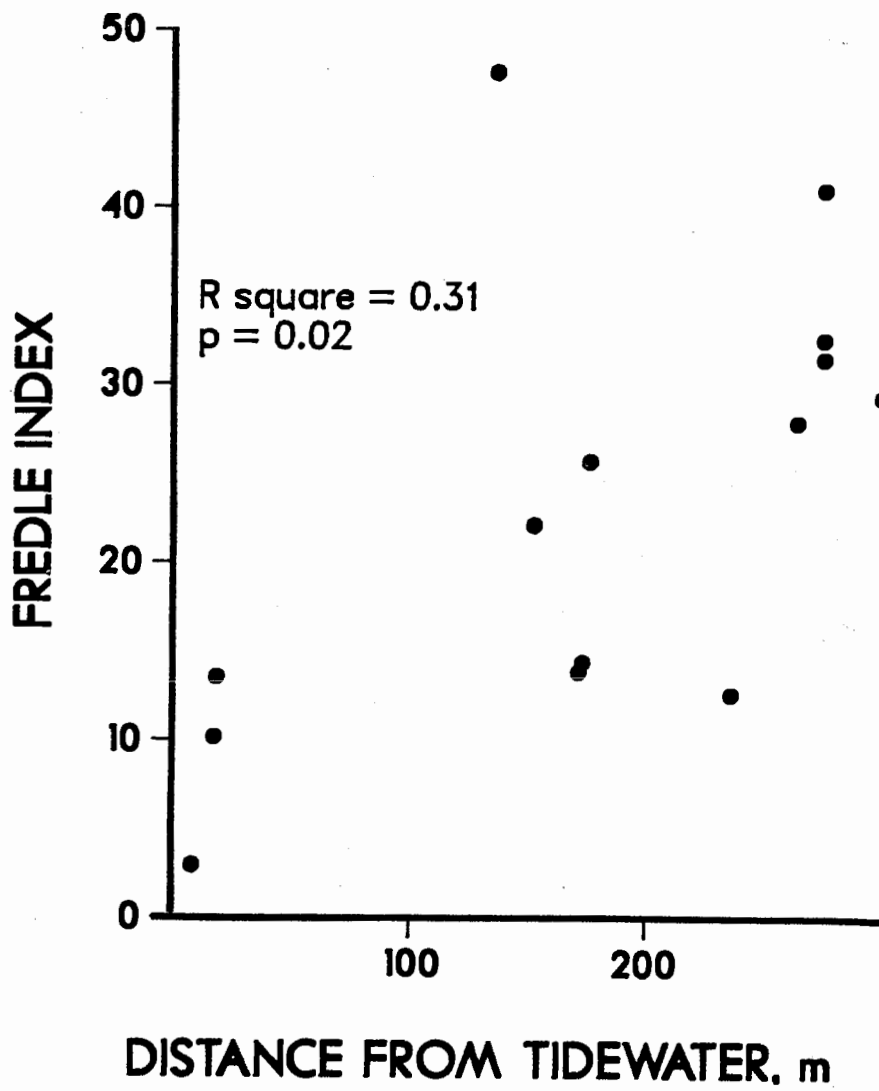
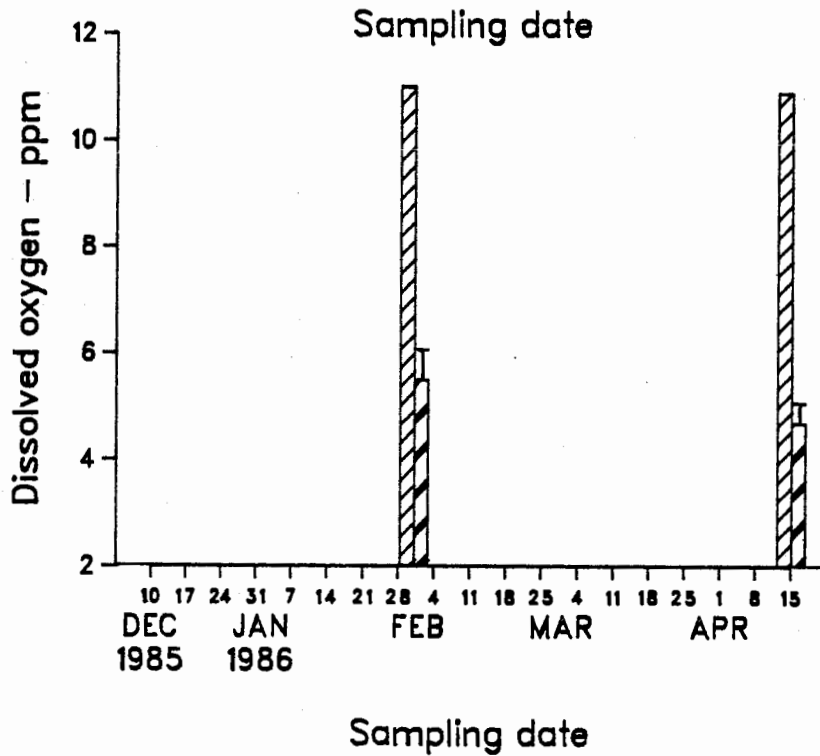
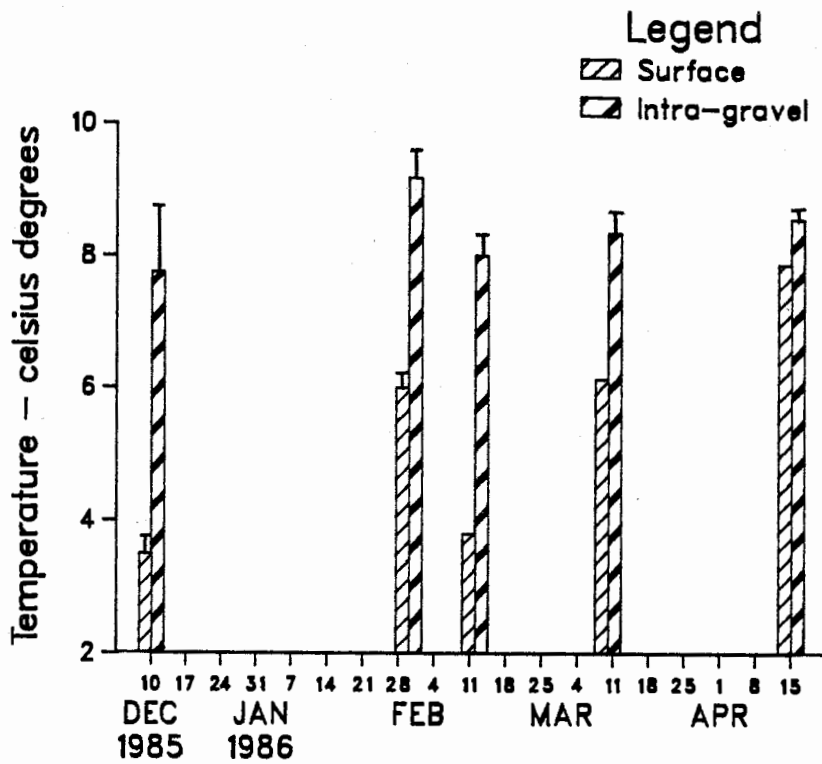


Figure 2.7: Intra-gravel and surface water temperature and dissolved oxygen at Walker Creek during 1985-1986. Standard error bars shown.



By examining substrate cores I was able to assess the mortality of chum salmon eggs during the period from fertilization to eye pigmentation. Clusters of eggs in substrate cores suffered either complete or negligible mortality, consequently mortality of eggs within substrate cores was assessed dichotomously as either complete or negligible. Of the 20 samples containing eggs, 3 (15%) suffered complete mortality and 17 (85%) samples had negligible mortality. Among those samples containing live eggs, a minority of the eggs had pigmentation in the eyes, but none had hatched. Nest sites suffering complete mortality had incubated at  $\bar{x}=6.3^{\circ}\text{C}$  whereas those that suffered negligible mortality had incubated at  $\bar{x}=8.5^{\circ}\text{C}$ , a significant difference (Mann-Whitney U test  $Z=2.20$ , d.f.=16,  $P=0.03$ ). There was also a significant difference in dissolved oxygen between those substrate cores that suffered complete mortality ( $\bar{x}=6.4$  ppm) and those that suffered negligible mortality ( $\bar{x}=4.8$  ppm), however, it was in a direction opposite to that anticipated (Mann-Whitney U test  $Z=1.98$ , d.f.=16,  $P=0.048$ ).

There were no apparent differences in morphology between the females whose eggs suffered complete and negligible mortality. However, females whose nests suffered complete mortality tended to be younger on average than those females whose nests suffered negligible mortality (Mann Whitney U-test,  $Z=2.38$ , d.f.=15,  $P=0.02$ ).



## *Nest dig-up and defense*

The incidence of nest dig-up was low in this study. Of the 65 nests constructed, only 3 (4.6%) were dug-up. Females that experienced nest dig-up defended their nests for less time ( $t=2.00$ ,  $d.f.=67$ ,  $P=0.025$ ), experienced higher female densities during their freshwater lifespan ( $t=10.4$ ,  $d.f.=55$ ,  $P<0.001$ ), built their nests in pools with higher local female densities ( $t=2.11$ ,  $d.f.=63$ ,  $P=0.04$ ), and at sites with greater water velocities ( $t=2.11$ ,  $d.f.=38$ ,  $P=0.04$ ), than did females whose nests were not dug-up (Table 2.1). Significant directional selection for longer nest defense by nest dig-up was not detected ( $n=68$ ,  $P=0.22$ ).

The date of arrival to spawn explained 15.1 % of the variation in the period of nest defense (Figure 2.8,  $r_a^2 = .15$ ,  $F=11.4$ ,  $d.f.=1,58$ ,  $P=0.001$ ). The inclusion of water velocity at the nest site into this regression as a second independent variable caused a further proportionate reduction in variation of 5.8% ( $r_a^2 = .20$ ,  $F=5.60$ ,  $d.f.=1,34$ ,  $P=0.008$ ) (defense =  $-.38$  arrival -  $.059$  velocity + 146). A partial regression of the period of nest defense on water temperature (averaged over the freshwater residence period) was not significantly negative ( $d.f. = 59$ ,  $P=0.5$ ).

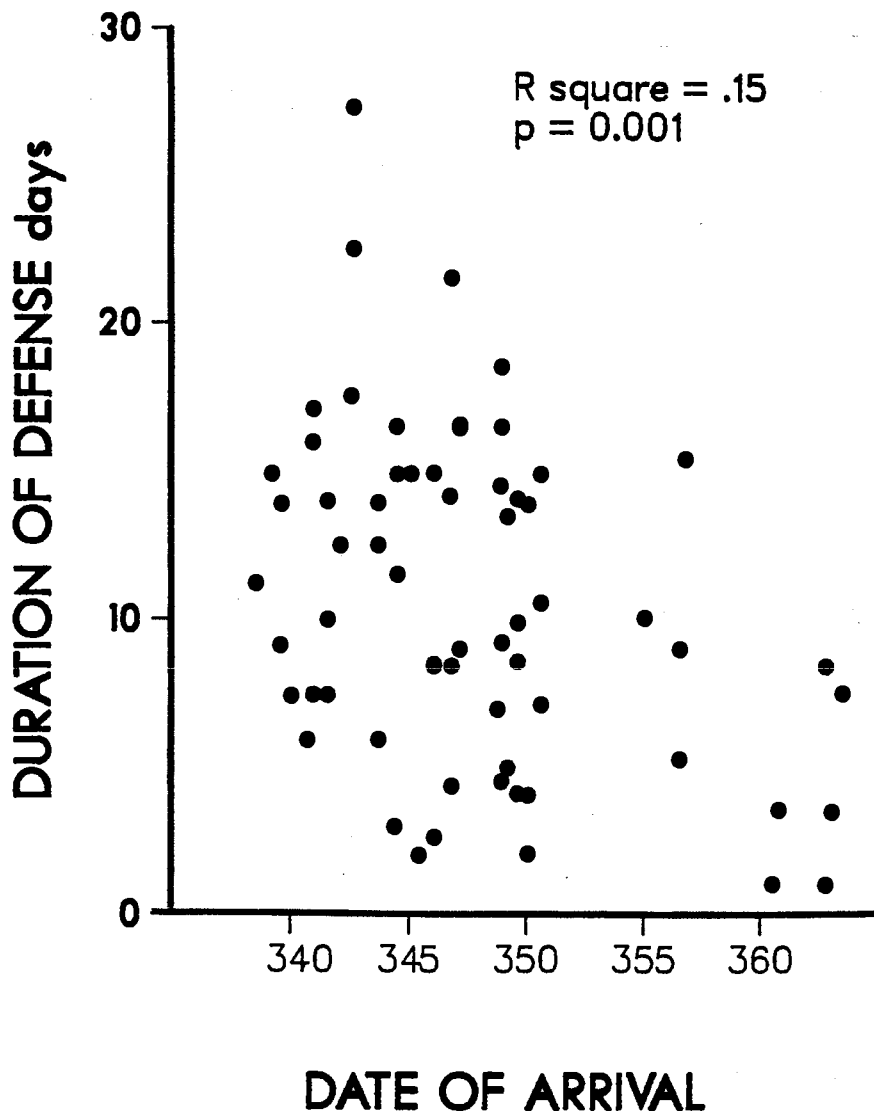
Contrary to predictions, neither mean spawner density during the period of stream residence ( $r=.104$ ,  $d.f.=62$ ,  $P=.41$ ) nor the frequency of competitive interactions per female per day ( $r=.03$ ,  $d.f.=59$ ,  $P=0.80$ ) were significantly correlated with the period

Table 2.1:

Females that did and did not experience nest dig-up:  
differences in behavior.

Variable	Nests not dug-up			Nests dug-up		
	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n
Female density ( $m^{-2}$ )	0.165	0.06	64	0.220	0.0170	3
Local density ( $m^{-2}$ )	0.257	0.198	62	0.500	0.0500	3
Nest defense (days)	10.3	5.73	66	3.65	1.49	3
Water velocity ( $cm\ sec^{-1}$ )	23.5	24.5	37	54.0	15.2	3

Figure 2.8: Duration of nest defense as a function of the arrival date to spawn.



of nest defense.

*Natural selection of arrival date*

No significant directional selection for arrival date by predation, competition for nest sites (egg retention), nest dig-up, scour, or incubation survival was detected. Arrival date was not normally distributed and could not be transformed in a manner that would be biologically interpretable. This prevented the measurement of disruptive and stabilizing selection. However, disruptive selection for arrival date to spawn probably occurs during competition for nest sites because mortality from egg retention and low nest site porosity are correlated with female density which is greatest near the middle of the arrival date distribution.

## Discussion

### *Habitat selection*

A branch of evolutionary theory, the theory of habitat selection, holds that the maximization of individual fitness should determine the dispersal and habitat selection patterns of animals (Whitham 1980). In an ideal free distribution all individuals settle in the habitat of their choice (Fretwell and Lucas 1970). In a despotic distribution, competitively superior animals monopolize the best territories, forcing some animals into territories that confer low fitness.

Female chum salmon in Walker Creek defended territories, and the spatial and temporal pattern of spawner distribution was consistent with this behavior. The distance of migration upstream was associated with female density upon arrival to the stream. Females abandoning their initial nest sites were those that experienced high female densities and arrival pulse sizes. Despotic distributions are also found among breeding female Pacific salmon from other species (Merrell 1962, McNeil 1966, Neilson and Banford 1983).

If natural selection molds behavior to enhance lifetime reproductive success, females should distribute themselves in response to female competition such that mean fitness within different habitat units (analogous to pools in this study) is equal (cf. Fretwell and Lucas 1970). The mean porosity within pools increased with increasing distance upstream in Walker Creek, suggesting that fitness was not equal between habitats.

However, there is a cost to the distance of upstream migration in terms of energy expenditure (Idler and Clemens 1969) and perhaps also in the risk of predation. The small discharge of Walker Creek made migration upstream difficult, consequently females were frequently seen stranded in riffles where the risk of predation might be greater. An hypothesis derived from the theory of habitat selection concerning female salmon behavior within Walker Creek is that females trade-off the cost of upstream migration with the expected survival at the nest site such that mean fitness in all pools is equal. Upon arrival, females had the option of migrating upstream to unoccupied areas or instead establishing territories in more densely occupied areas. Females migrating further upstream to construct their nest experienced a lower within-pool density at the time of nest construction, and as a result obtained a territory of higher porosity than available further downstream.

Nest site porosity is correlated with egg survival among coho salmon (Lotspeich and Everest 1981), however its effect on survival was not measured here. Nest site porosity was greater among those females whose nests avoided scour, but this may be a spurious result since substrate samples were collected after scour had occurred. Egg survival during incubation was not related to substrate porosity possibly because survival was assessed at eye pigmentation, while the period of oxygen demand prior to hatching is more sensitive to low dissolved oxygen (Alderdice et al. 1958). The lack of association here between egg survival and porosity could result from the overall high

porosity of Walker Creek substrate as described in Chapter 1 (83% of the nest sites had porosity that would confer over 80% survival to coho salmon eggs). High porosity suggests low levels of mortality, perhaps sufficiently low to escape detection using the dichotomous method of mortality assessment applied here.

Female salmon do not always choose substrate of high porosity in which to spawn. Female chum salmon in Big Beef Creek, Washington, chose substrate of intermediate particle size (Duker 1977) suggesting that high mortality may be associated with high porosity in some situations. Phillips and Claire (1966) state that Pacific salmon eggs experience high mortality in very porous substrates because predators (sculpins) can easily reach incubation areas.

#### *Nest defense*

Selection of longer nest defense time was not detected, although females whose nests were dug-up experienced higher female density than those females who avoided nest dig-up. Selection may not have been detected because so few nests were dug-up, yielding a small sample size for analysis. Factors that may contribute to the lack of selection on nest defense are that nest dig-up was infrequent and that females with short periods of nest defense arrived late in the season when the risk of nest dig-up was lowest. McNeil (1964) hypothesized that the progeny of early arriving females would experience the most mortality as a result of nest dig-up, however the present study is contrary to this hypothesis, likely as a result of the long nest defense



by early arriving females.

Contrasting the results of the present study with those of Schroder (1973, 1981) makes clear the importance of nest defense as a deterrent to nest dig-up. Schroder (1973) stocked artificial spawning channels with varying densities of spawners with the same period of nest defense and then observed their nest site locations. Schroder observed an increase in the frequency of dig-up with increasing spawner density. Applying this relationship to the present study, we predict that at the observed average density of  $0.31 \text{ m}^{-2}$ , 11.9% of the nests should experience dig-up. However, the percentage of nests dug-up in the present study was only 4.6%. The low rate of dig-up is likely due to the lengthy nest defense by early females which forced the upstream migration of later arrivals. Thus, in the wild, behaviors exhibited by early arriving females appear to reduce the likelihood of nest dig-up.

Temporal patterning in the intensity of expression of traits beneficial in competition was predicted. Early arriving females defended their nests longer than later arriving females, thus behavior exhibited temporal patterning in expression, however, body size and morphology did not (Chapter 1).

#### *Arrival date to spawn*

Females spawning at high female densities experience a higher egg retention and lower nest site porosity which may cause disruptive selection for arrival date. While nest dig-up exhibited no temporal trends in the present study, it did cause

directional selection for later spawning in a controlled experiment with rainbow (Salmo gairdneri) and brown trout (Hayes 1987). This suggests that females arriving to spawn at the end of the run experience the least female competition, however the lack of females arriving at this time suggests that some selective disadvantage exists to very late spawning which counteracts the advantages gained by relaxed female competition.

One of the disadvantages to late spawning could be the effect it has on juvenile emergence timing. Bams (1969) suggested that adult spawning could be timed such that juvenile arrival to the estuary was optimized. Walters et al. (1978) suggest that an optimal time of arrival to the estuary for chum salmon fry exists such that fry entering the estuary before or after the optimal date experience lower zooplankton abundance which leads to slower growth. Slower growth results in smaller size, which in turn increases mortality, possibly by increasing the time fry spend in predation-prone size ranges (Healey 1982). Late arrival to spawn could result in late fry arrival to the estuary if a limit exists to how rapidly an egg can develop, however, there is no evidence that a limit to the rate of development exists. Heritable variation in egg development rate exists among chum salmon (Tallman 1986), consequently adult spawning time and juvenile emergence time should be free to evolve independently to some extent.

Another effect of late spawning could be lower egg survival from the effects of lower incubation temperatures. Chum salmon eggs that experienced high mortality during the present study

incubated in nest sites with cooler temperature regimes than did those eggs experiencing low mortality which incubated at sites strongly influenced by the warm ground water present at Walker Creek. Cold water incubation regimes are a well know cause of mortality to chum salmon eggs during their early development (Combs and Burrows 1957, Beacham and Murray 1987a, 1987b), however their tolerance to low temperatures increases once the initial period of cell division is completed (Burrows 1963, Bailey and Evans 1971), although this tolerance varies between stocks and families within stocks (Beacham and Murray 1987b). A further impact of cold initial incubation temperatures is abnormally slow development which results in delayed emergence (Alderdice and Velsen 1978). Several studies have reported a negative correlation between time of spawning and egg survival within populations of pink salmon between years (Skud 1958, Merrell 1962, Heard 1978) and this has been attributed to the negative effects of cold water on the eggs of late spawners (Merrell 1962). While adaptation to incubation temperature occurs, almost all stocks in southern British Columbia experience the highest mortality at 2°C (Beacham and Murray 1985c), which is close to the average stream water temperature at Walker Creek during initial incubation in 1985 ( $\bar{x}$  = 2.4°C). The presence of warm ground-water in Walker Creek substrate allows eggs to incubate at temperatures above those causing mortality and still spawn later in the year, when cold stream water temperatures persist, than do populations in most other streams on southern Vancouver Island (Marshall et al. 1979). The association of spawning chum salmon with areas of warm upwelling

groundwater is common wherever stream water is cold; in Arctic streams (Kog1 1965, Milligan et al. 1984, Smirnov 1976) and late spawning populations in southern areas (Schubert 1982).

Dissolved oxygen in warm groundwater was low enough ( $\bar{x}=4.9$  ppm at  $8^{\circ}\text{C}$ ) to cause hypoxic stress to chum salmon eggs during the observed period of development (to eye pigmentation) according to some studies and was below the level of 50% morality (stress at 6.5 ppm at  $10^{\circ}$  after 350 degree days, Alderdice et al. 1958). In the present study egg mortality increased with increasing dissolved oxygen, suggesting dissolved oxygen sufficient for survival. Average nest depth was less than the 20 cm depth groundwater samples were taken at, so dissolved oxygen was likely greater than measured, while temperature was likely less than measured. Another factor contributing to the low mortality may have been the high tolerance of chum salmon eggs to low dissolved oxygen in cold water. Kog1 (1965) found no egg mortality at dissolved oxygen as low as 2.0 ppm (at 3 to  $5^{\circ}\text{C}$ ) among Alaskan chum salmon incubating in groundwater and Levanidov (1954) reports chum salmon eggs can survive dissolved oxygen at 0.5 ppm.

Many factors influence the mortality and reproductive success of female salmon arriving to spawn at different times. Gilhousen (1960) hypothesized that the dispersion of spawning may be determined by the shape of the survival versus arrival date function. I contend that the present pattern of arrival to spawn is a result of the effect of both female competition and abiotic factors. Female competition for nest sites results in

nest dig-up which causes directional selection for late spawning, while incubation temperature regimes constrain how late spawning can be. Simultaneously frequency-dependent disruptive selection for arrival date favors the evolution of multiple arrival dates within these constraints on extremely early or late arrival to spawn. Natural selection requires heritable variation in fitness within a trait. Whether the date of arrival to spawn is heritable among chum salmon is not known, however it is heritable among pink salmon (Bams 1976, Taylor 1980) and steelhead trout, Salmo gairdneri (Leider et al. 1984).

Other factors influence the fitness of females spawning at different times. Seasonal variation in risk of predation by marine mammals (Mate (in press) cited in Fiscus 1981) and humans (Anderson and Beacham 1983) is known to exist. Mortality of adults due to unfavorable river discharge and temperature may affect reproductive success in a temporal fashion (Murphy 1985). The present study illustrates the role of female competition in the selection for particular arrival date phenotypes.

The magnitude of mortality through female competition relative to other sources of mortality is of interest because the mode of natural selection (directional, stabilizing, or disruptive) operating on arrival date will be determined by the sum of all mortalities and the reproductive success. The Johnstone Strait area of British Columbia experienced chum salmon exploitation rates of 50% in the 1950's; presently they range from 20% to 40% (Anderson and Beacham 1983). In this study egg mortality from female competition was 12.4%; 4.6% from nest

dig-up and 7.8% from egg retention. Fishing mortality is greater than mortality caused by female competition, probably because present spawner densities are less than those in the 19th century, which itself is a result of fishing mortality (Hoar 1951).

The current frequency distribution of arrival date found in Walker Creek could be a result of mortality through fishing, however some evidence supports the idea that Walker Creek chum salmon escape commercial fishing. Virtually all migration of chum salmon to the east coast of Vancouver Island occurs through Johnstone Strait, where late arriving runs experience a lower exploitation rate than do early arriving runs (Anderson and Beacham 1983). The Walker Creek run arrives to spawn later than most other runs in Johnstone Strait (Marshall et al. 1979). During the period of 1967-1970 the Walker Creek peak arrival date (julian day 339) lagged after the latest fishery opening (day 303) by a period longer than the average duration of migration through Johnstone Strait (30 days) (Anderson and Beacham 1983). This suggests no interception by the commercial fishery. If the fishery does capture Walker Creek chum salmon, it likely does so at the beginning of the run and, in isolation, would cause directional selection for late arriving females. Thus fishing mortality probably plays a small role in maintaining the current frequency distribution of arrival date to Walker Creek.

Temporal aggregations may be maintained by the behavioral mechanisms of photoperiod and temperature response during the

marine lifestage (Whitehead et al. 1978, Burgner 1981). Several accounts of how stream discharge, temperature and turbidity influence the immigration of spawning salmon on a proximate level exist (Pritchard 1937, Hunter 1959, Sano 1966, Mayama 1978). Date of arrival to spawn among Pacific salmon has been negatively correlated with spawner abundance (Helle 1979, Beacham and Starr 1982), positively correlated with ocean surface temperatures (Blackbourn 1987) and negatively correlated with inshore air temperatures (Burgner 1981, Mundy 1982). Further, date of arrival to spawn is both negatively and positively correlated with body length (Skud 1958, Pritchard 1937, respectively) and negatively correlated with age at maturity within some populations (Marr 1943, Hunter 1959, Mattson and Rowland 1963, Helle 1979). Further work is needed to determine the environmental and genetic variance components of phenotypic variance in arrival date to spawn. This will allow a more precise assessment of the relative roles of female competition, predation, and fishing mortality in the natural selection of temporal patterns of spawning among Pacific salmon.

## CHAPTER III

# INTERSPECIFIC BREEDING COMPETITION AND SEGREGATION OF SPAWNING BETWEEN FEMALE CHUM AND COHO SALMON.

### Introduction

A review of the literature on competition has shown that it is difficult to produce clear demonstrations of interspecific competition (Connell 1983). Nevertheless, interspecific breeding competition among members of the genus Salmo in man-induced sympatry clearly caused mortality and resultant natural selection of particular spawning times (Hayes 1987). Other studies of introduced salmonid species have shown some evidence of interspecific breeding competition (Witzel and Macrimmon 1983) while studies of native species have found insignificant competition (Crone and Bond 1976).

Pacific salmon spawning at high densities could compete for territories or avoid interspecific competition through spatial or temporal segregation of spawning. In this study I examine competition for spawning sites between female chum and coho salmon, which I define as contests for spawning territories and nest dig-up. I also examine segregation of spawning in time and space, measure nest site characteristics important to egg survival, and compare between species egg mortality during scour and incubation. Finally, I discuss how relationships between morphology and physical variables important to survival during incubation vary between species.



Pacific salmon species frequently use the same river for spawning but may avoid competition for spawning sites through temporal segregation. However, temporal segregation must be great to avoid competition, as interference competition for nest sites among salmon can occur through dig-up of undefended nests by late spawning females, since eggs and alevins persist in the gravel for long periods. For example, chum salmon from the Vedder River B.C. take 126 days to reach 50% hatch at 4°C (Beacham and Murray 1985c). Thus, in order for species to utilize the same spawning area without competing for spawning space, the timing of spawning would have to differ in the order of seasons.

Pacific salmon are widely distributed geographically and the spawning sites of different species can be spatially isolated. Part of the rationale for stream and even site-specific homing of salmon is that it allows adaptation to local environments and local adaptation as has been found within species of Pacific salmon (Ricker 1972). Some potential adaptations to local environments which will be investigated here are egg size, development rate, female size, and the relationship between female size and egg size. The greater surface area to volume ratio of small eggs allows them greater survival than large eggs in low porosity substrate (van den Berghe and Gross 1984). Eggs incubated for long periods are larger than those that incubate for short periods, presumably because they need more nutrients to survive the longer incubation (Beacham and Murray 1985c).

Large body size may be advantageous in large streams (Beacham and Murray 1984a, 1987a) and possibly also when competition for nest sites is intense (present study Chapter 1, van den Berghe and Gross 1987).

The relationship between female size and egg size varies between populations, possibly as a result of variation in gravel composition and the intensity of competition (Fleming and Gross 1987a). If the relationship between female size and egg size has evolved in response to variation in gravel composition and female competition, it follows that in streams where substrate porosity is high and little variation in survival during incubation exists, overall egg size should be large (Holtby and Healey 1986), and egg size should vary little with body size, since egg size would not be constrained by gravel porosity. Where substrate porosity is low and there is large variation in survival during incubation, overall egg size should be small (Holtby and Healey 1986), and strongly positively correlated with female body size, since egg size is constrained by porosity and female competition results in large females obtaining the high porosity nest sites.

## Methods

Studies were conducted as described in chapter 1 for chum salmon. Measurements on coho salmon were as follows: in 1984, 1985 and 1986 adult coho salmon were captured upon arrival at the fence and their sex recorded. The fork length ( $\pm 0.05$  cm) of

coho salmon females was recorded. A small sample of female coho salmon was retained for a Salmonid Enhancement Program (S.E.P.) project at Mountdale Farms, Ladysmith, B.C. in 1985. The fork and postorbital-hypural length ( $\pm 0.05$  cm) and fecundity of these females was measured and scales were taken from between the dorsal fin and lateral line for aging. A sample of 30 eggs was collected from individual chum and coho salmon immediately after capture. These eggs were water hardened for one hour and preserved in 5% formalin in Ringer's solution (6.0 g NaCl, 0.20 g Na<sub>2</sub>CO<sub>3</sub>, 0.14 g KCl, 0.12 Ca<sub>2</sub>Cl /litre, 5% formalin). After storage at 2-20 °C for 3 months, eggs were dried at 92 °C for 36 hours, and immediately transferred to an airtight container lined a drying compound (calcium sulphate) and were weighed ( $\pm 0.0001$  grams) individually within 24 hours.

Ages were read by the author and are presented in the North American format (Gilbert and Rich 1927).

Coho salmon eggs collected for the S.E.P. at Mountdale Farms incubated in heath trays in water of constant temperature from a groundwater source at Mountdale Farms in 1985 and 1986. Eggs were checked for mortality and developmental state every 3 days. Eggs from 14 chum salmon females taken in 1986 were incubated in the same manner as the coho salmon. This provided data on survival at constant temperature, as well as the time and thermal units to hatch.

The behavior of female salmon was observed daily during the period that they occupied Walker Creek (December 5 1985 to

January 10 1986). The location of redds observed being constructed or defended by female coho salmon were marked with a line suspended from shore and over the centre of the redd. As described in chapter 1, the oxygen and temperature at 20 cm below the substrate surface was measured at known coho salmon nests and a sample of the substrate was taken at these nests and the porosity measured in the lab.

## Results

### *Timing and abundance of adult salmon spawning migration*

The escapement of adult female salmon to Walker Creek varied between years and between species. Table 3.1 illustrates the annual escapements above the fence and shows that chum salmon were numerically dominant. The number of female chum and coho salmon that spawned below the fence in all three years was estimated by foot survey: chum, <50 in 1984, <20 in 1985 & 1986, and coho <5 in all three years.

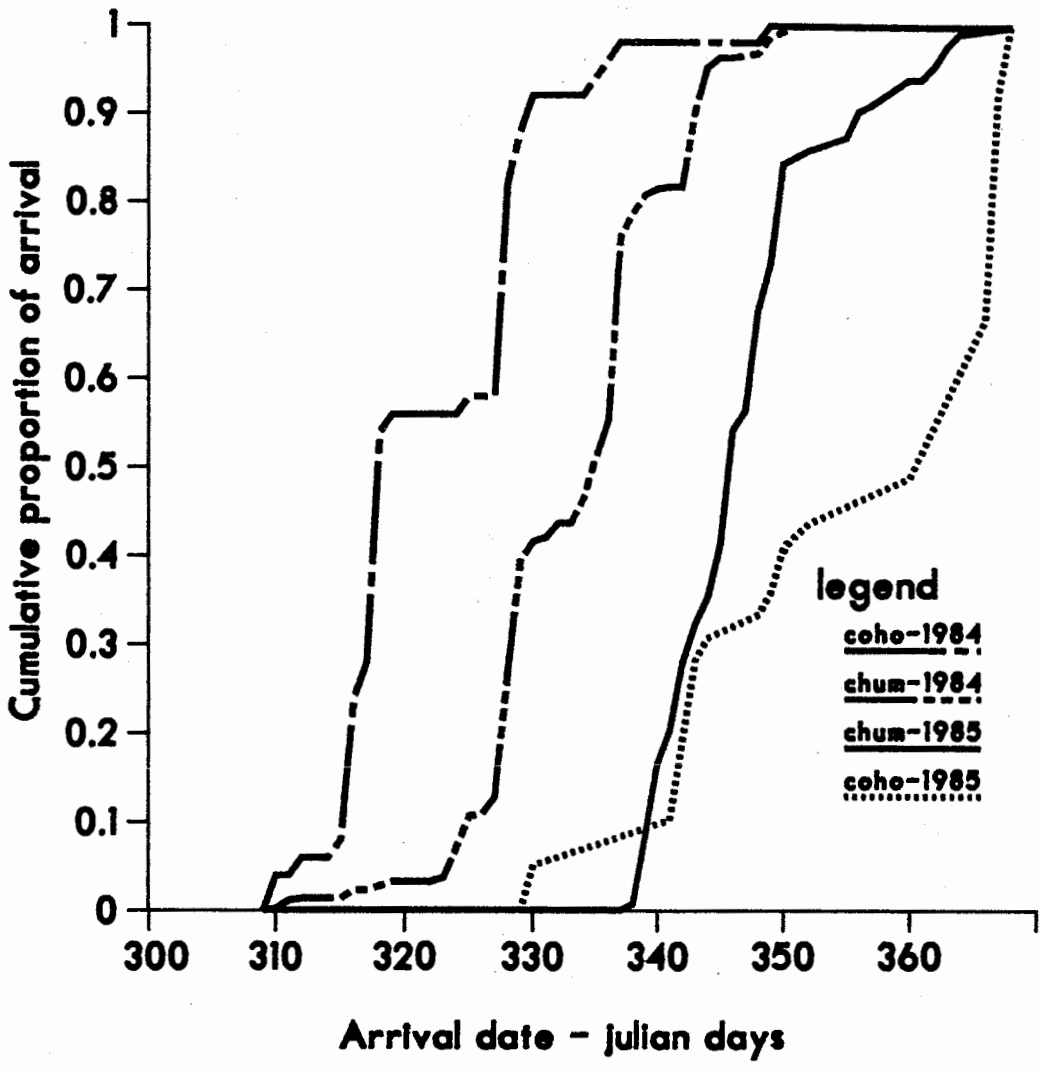
Figure 3.1 illustrates the distribution of arrival dates for chum and coho salmon in 1984 and 1985 respectively. Among both species arrival to spawn was not uniform but occurred in a series of pulses. In both years the arrival distribution of female chum salmon was significantly non-normal, with a slight negative skew in 1984 and a positive skew in 1985. The arrival distribution of female coho salmon was also non-normal in both years. Both species arrived to spawn earlier in 1984 than in 1985, possibly because mean stream discharge during November,

Table 3.1: Escapement of female chum and coho salmon to Walker creek in 1984, 1985 and 1986.

Year	Chum salmon	Coho salmon
1984	420	49
1985	138	37
1986 <sup>1</sup>	36	6

<sup>1</sup>Fence vandalized, fence counts inaccurate.

Figure 3.1: Cumulative arrival dates to spawn for female chum and coho salmon in 1984 and 1985.



1984, was  $0.28 \text{ m}^3\text{sec}^{-1}$  but in November, 1985, was only  $0.03 \text{ m}^3\text{sec}^{-1}$ . Female coho salmon arrived to spawn earlier than female chum salmon in 1984, but later in than female chum salmon in 1985.

#### *Incubation rate*

Coho salmon returning to spawn in 1985 took 69 days to hatch at  $7.5^\circ\text{C}$ . Chum salmon returning to spawn in 1986 took 70 days to hatch at  $7.5^\circ\text{C}$ . The measurement error of the data ( $\pm 1.5$  days) was sufficient to cause an overlap of the mean estimated times to hatch.

#### *Age, body size, and egg size*

The scales of 6 female coho salmon were examined, all were age 3. The scales of 182 female chum salmon were examined over 3 years and the percentage of each age was; age 3 - 44.9%, age 4 - 54.4%, age 5 - 1.6%).

Over all three years (1984-1986), female coho salmon had a smaller mean fork length than female chum salmon (Table 3.2,  $t=4.87$ ,  $d.f.=246$ ,  $P<0.001$ ), even when only age 3 female chum salmon are considered ( $t=2.05$ ,  $d.f.=107$ ,  $P=0.04$ ). In 1985 alone coho salmon had a smaller fork length ( $t=4.36$ ,  $d.f.=149$ ,  $P<0.001$ ), however there was no significant difference when only age 3 female chum salmon are considered ( $t=1.06$ ,  $d.f.=59$ ,  $P=0.3$ ).

The fecundity and egg weight of 21 chum salmon and 6 coho salmon taken from Walker Creek in 1985 were compared (Table



3.2). Within this sample, coho salmon were smaller in postorbital-hypural length, although not significantly so, ( $t=1.94$ ,  $d.f.=25$ ,  $P=0.06$ ) and had significantly lighter eggs ( $t=2.96$ ,  $d.f.=25$ ,  $P=0.007$ ), however their fecundity was not significantly different than that of chum salmon ( $t=0.77$ ,  $d.f.=18$ ,  $P=0.453$ ).

*The relation between fecundity, egg size and body size*

Fecundity and dry egg weight increased with postorbital-hypural length among both chum and coho salmon (Figure 3.2). Fecundity increased with the cube of body length for both species, i.e. the exponent of the power function was not significantly different from 3 (Table 3.2). However, among chum salmon dry egg weight increased at less than the cube of body length while among coho salmon egg size increased with the cube of body length.

*Spatial pattern of stream use*

Of 745 meters of stream that was accessible to chum and coho salmon in 1984 and 1985, 125 meters was located below the fence and the majority of this was intertidal. In 1984 both species used the entire accessible length of stream (Figure 3.3). In 1985, spawning chum salmon were found in significant concentrations only in the lower 300 meters of stream whereas coho were widely dispersed throughout the entire stream (Figure 3.4).

Table 3.2:

Differences between chum salmon and coho salmon females in fork length, postorbital-hypural (POH) length, fecundity, egg size and in the geometric mean (GM) regressions of fecundity and egg size on POH length.

Comparison of means

Character	Chum salmon			Coho salmon		
	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n
Fork length (cm) <sup>1</sup>	68.8	4.97	219	64.0	4.91	29
Fork length (cm) <sup>2</sup>	68.3	4.89	133	63.0	4.70	18
POH length (cm)	54.0	3.71	19	50.9	2.30	6
Fecundity	2421	826.9	14	2130	638.3	6
Egg weight (mg) <sup>3</sup>	0.238	0.027	21	0.198	0.035	6
Mean age	3.5	0.519	14	3.0	00.0	8

<sup>1</sup> data from 1984-1986

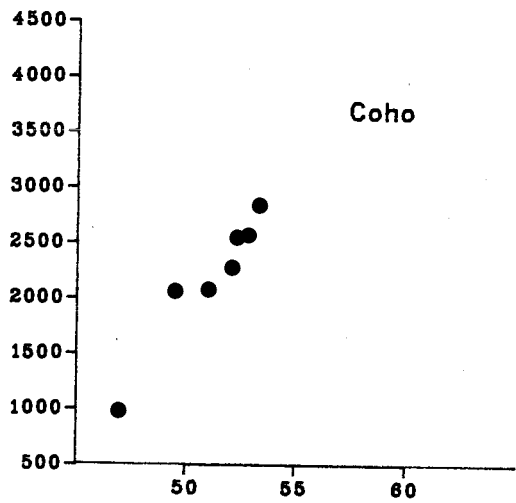
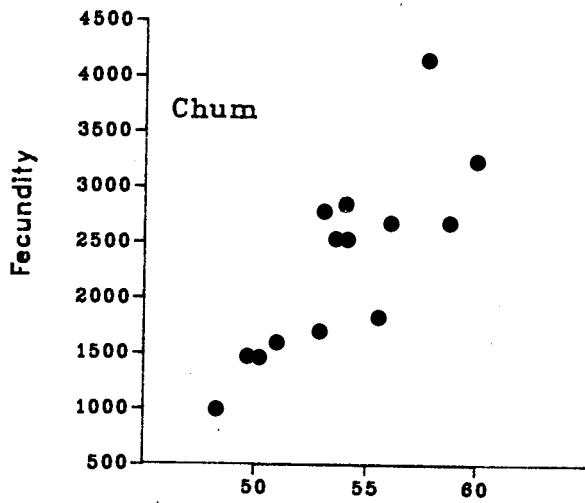
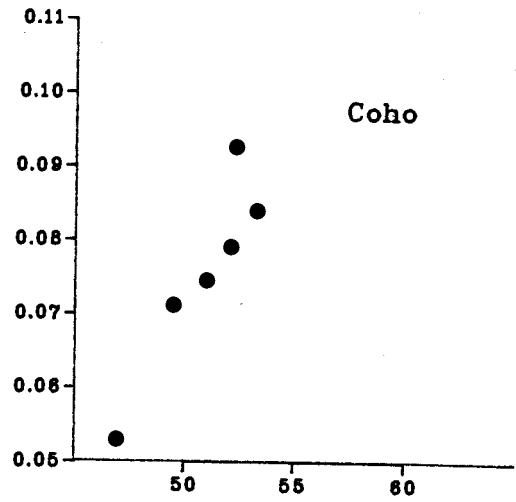
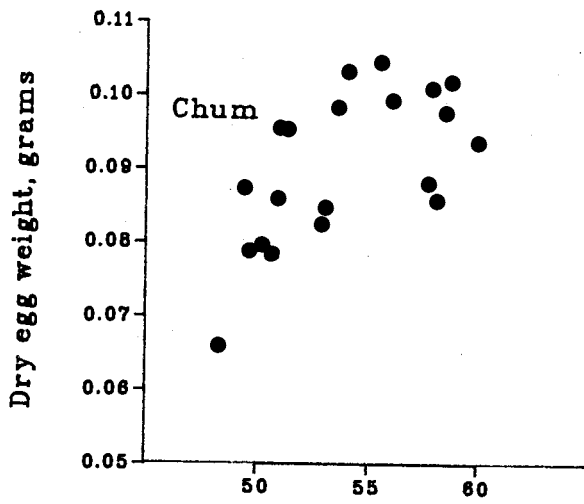
<sup>2</sup> data from 1985

<sup>3</sup> each sample point a mean of 30 individual egg weights

Comparison of GM regressions on POH length ( $y=a(\text{POH length})^b$ )

Variable	n	a	b(±C.I.)
Dry egg weight			
Coho	6	$4.8 \times 10^{-5}$	$4.83 \pm 1.98$
Chum	17	$7.0 \times 10^{-7}$	$1.76 \pm 0.72$
Fecundity			
Coho	6	$7.0 \times 10^{-16}$	$8.24 \pm 5.44$
Chum	29	$4.7 \times 10^{-9}$	$4.20 \pm 1.45$

Figure 3.2: Dry egg weight and fecundity of chum and coho salmon versus postorbital-hypural length.



Postorbital-hypural length

Figure 3.3: Distribution of chum and coho salmon spawning sites in 1984.

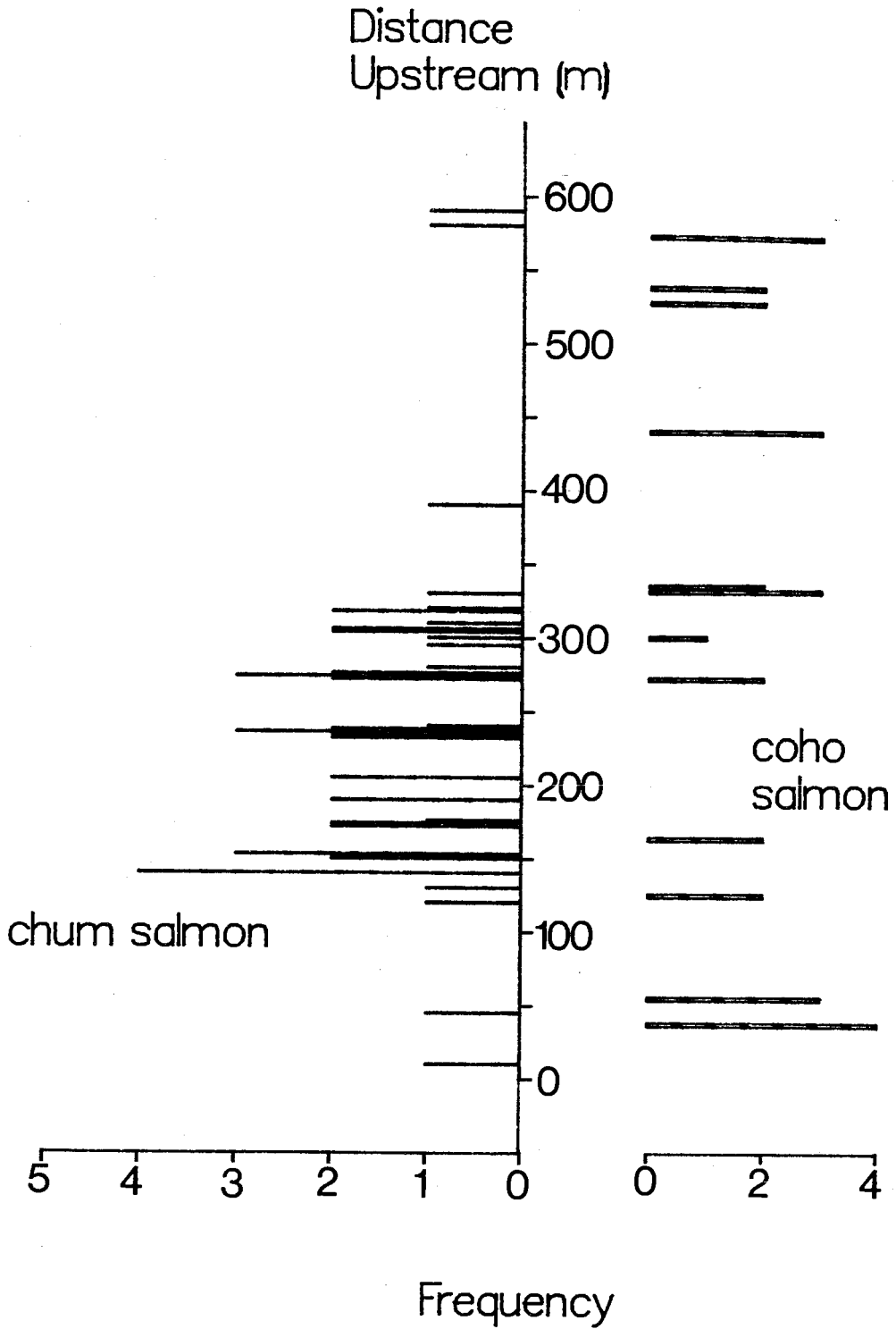
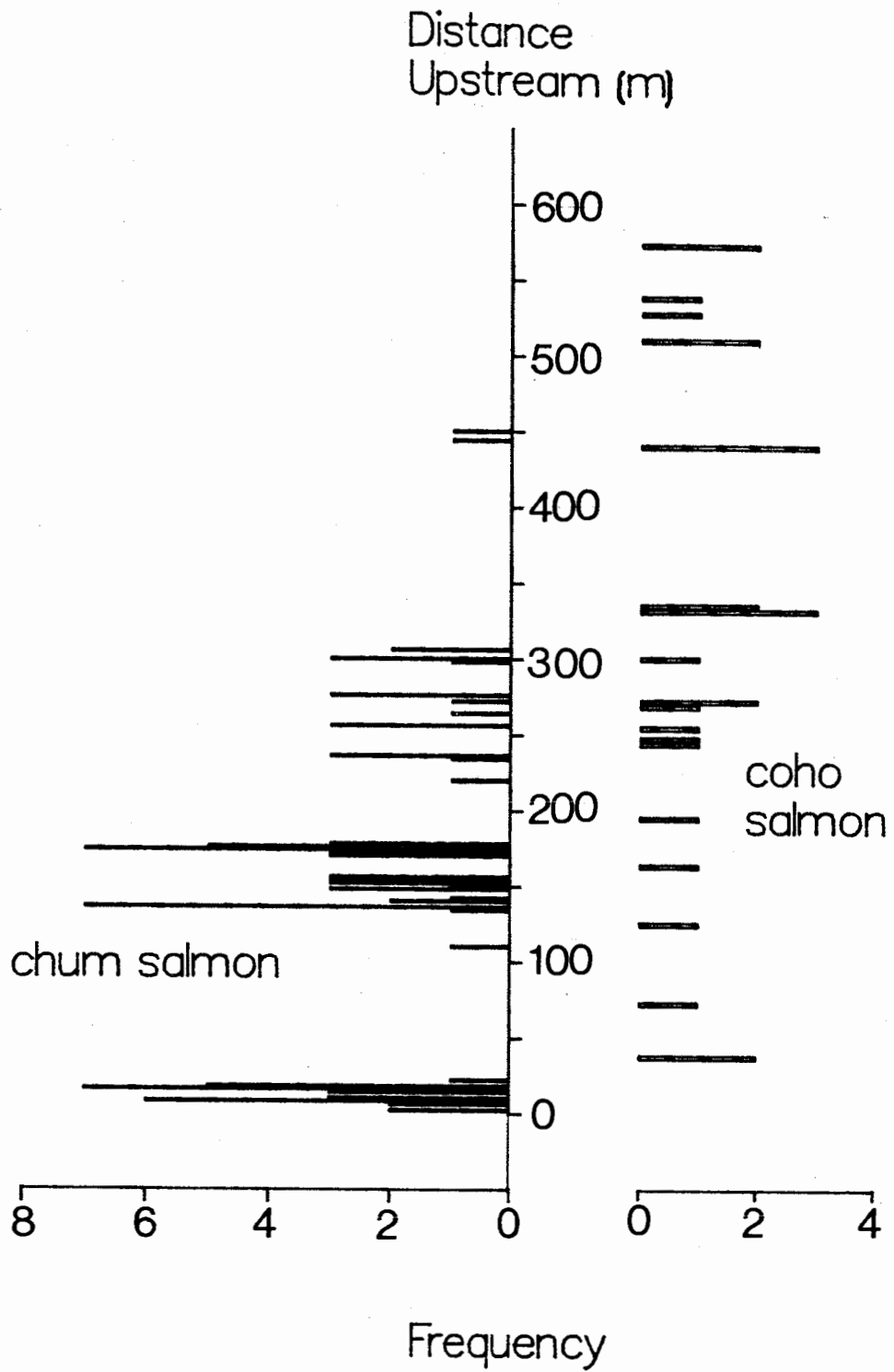


Figure 3.4: Distribution of chum and coho salmon spawning sites in 1985.





## *Physical characteristics of spawning sites*

Eighty-one chum salmon and 27 coho salmon were observed defending territories over redds in 1985. While both chum and coho salmon were seen spawning in riffles in Bush Creek, the watershed adjacent to Walker Creek, Walker Creek riffles were too shallow to allow spawning ( $< 10$  cm depth). Consequently both species spawned predominantly in pools, in water depths greater than 13.7 cm (chum salmon) and 12.2 cm (coho salmon). While the mean water depth of redds did not differ significantly (d.f. = 63,  $P=0.13$ ) between chum and coho salmon, other microhabitat parameters did (Table 3.3). Chum salmon spawned in pools with a larger surface area than did coho salmon (Mann Whitney U-test,  $Z=4.22$ ,  $P<0.0001$ ,  $n=113$ ). Also, chum salmon were distributed throughout pools whereas coho tended to locate at pool outlets, where the stream channel narrowed, consequently the water velocity at the redd site was significantly slower among chum salmon than coho salmon ( $t=2.19$ , d.f.=63,  $P=0.03$ ). Cover in wood debris and undercut banks was abundant in Walker Creek and present wherever salmon spawned.

The substrate and incubation water characteristics of chum and coho salmon nests differed (Table 3.3). Chum salmon built their redds in gravel of greater porosity than did coho salmon ( $t=1.71$ , d.f.=27,  $P=0.10$ ), although not significantly so, while coho salmon eggs tended to be buried more deeply ( $t=1.82$ , d.f.=27,  $P=0.08$ ), but again not significantly so. The intra-gravel water incubating coho salmon eggs was more like stream water in its temperature and dissolved oxygen than was

Table 3.3:  
Differences between chum salmon and coho salmon in nest site characteristics and egg burial depth.

Variable	Chum salmon nests			Coho salmon nests		
	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n
Pool surface area (m <sup>2</sup> )	69.6	37.7	86	47.6	53.0	27
Water velocity (cm sec <sup>-1</sup> )	23.7	23.8	51	39.8	26.7	14
Water depth (cm)	27.2	13.2	51	21.0	14.1	14
Porosity (fredle index) <sup>1</sup>	21.61	12.46	21	13.29	9.190	8
Temperature (°C) <sup>2</sup>	8.20	1.29	140	6.44	1.49	28
Dissolved oxygen (ppm) <sup>2</sup>	4.75	1.20	53	7.12	2.77	9
Egg burial depth (cm)	13.4	6.04	21	18.1	6.71	8

<sup>1</sup> upper substrate layer, 15 cm thick

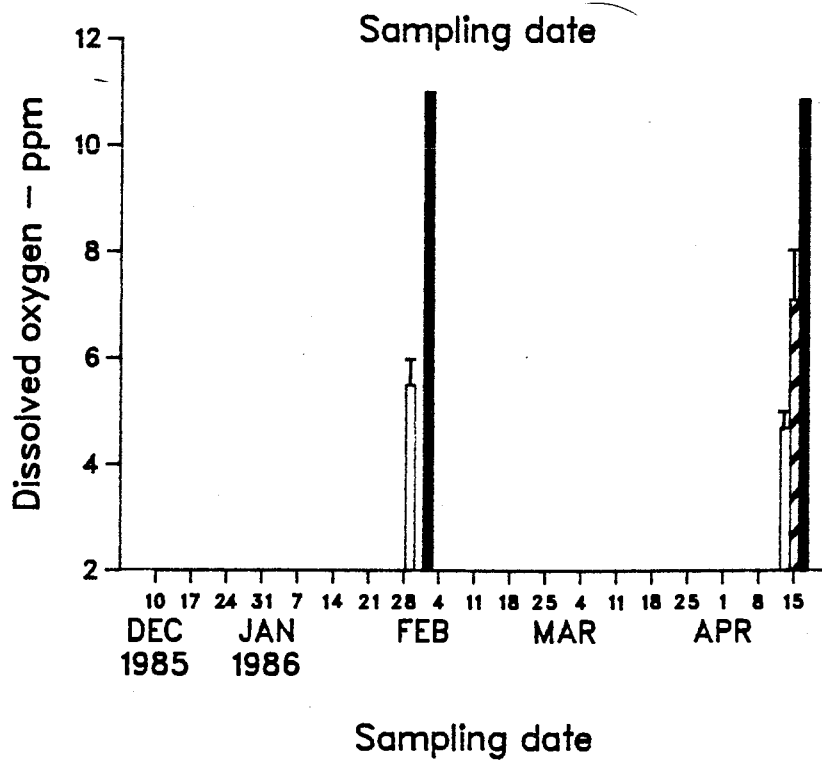
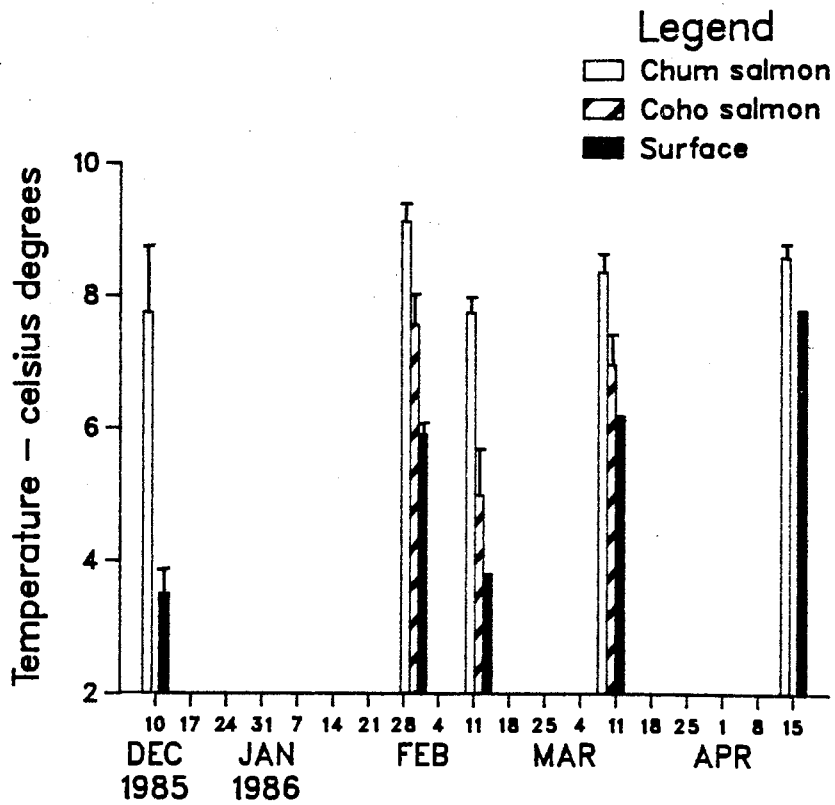
<sup>2</sup> 20 cm below substrate surface

water incubating chum salmon eggs (Figure 3.5). The dissolved oxygen 20 cm below the substrate surface was greater at coho salmon redds than at chum salmon redds (March 15 1986, t-test  $t=2.53$ , d.f.=9,  $P=0.03$ ). The temperature at 20 cm below the substrate surface was greater at chum salmon redds than at coho salmon redds on the 3 occasions they were compared; January 30 1986 ( $t=5.87$ , d.f. =29,  $P<0.001$ ), February 12 1986 ( $t=5.23$ , d.f. =70,  $P<0.001$ ), March 10 1986 ( $t=5.11$ , d.f. = 59,  $P<0.001$ ).

Substrate samples that contained no eggs but were taken at known nest sites were considered scoured. Twenty-one out of 41 (51%) chum salmon nests and 3 out of 11 (27%) coho salmon nests were scoured, likely as a result of high water discharges. In addition, 4 known coho salmon nests were completely washed out to the extent that no gravel remained to take a sample of, giving a scour rate of 47%. Nests that survived scour and contained eggs either experienced complete or negligible mortality. Three out of 21 (14%) samples containing eggs taken at chum salmon nests experienced complete egg mortality while none of the 8 coho nests sampled experienced mortality.

While chum salmon nests that experienced nest scour had lower fredle indices and experienced more rapid water velocities (Chapter 1), no such differences were detected between coho salmon nests that did and did not experience nest scour (Mann Whitney U, porosity;  $Z=.41$ , d.f.=9,  $P=.68$ , water velocity;  $Z=.61$ , d.f.=9,  $P=.54$ ).

Figure 3.5: Intra-gravel and surface water temperature and dissolved oxygen at Walker Creek during 1985-1986 for chum and coho salmon. Standard error bars shown.



## *Competition for nest sites*

Eleven contests between chum and coho salmon females were observed during 1822 behavioral observations. In contrast, 79 contests between chum salmon females were recorded, undoubtedly as a result of their greater abundance. Nine interactions were recorded between territorial chum salmon and intruding coho salmon females and all were won by chum salmon. Three contests between territorial chum salmon and territorial coho salmon females were observed and chum salmon females won one, lost one and tied one. Three coho salmon females were able to establish territories among territorial chum salmon females, suggesting that they were not competitively inferior to chum salmon. The outcomes of contests between females are likely to depend on ownership, female size, and the quality of available territories, as discussed in Chapter 1.

Five interspecific and 4 intraspecific nest dig-ups were observed in 1985. Four of the 65 (6.2%) known chum salmon nests were dug up by coho salmon, while only 1 of the 27 (3.7%) nests defended by coho salmon was dug up by a chum salmon. Three of the territory takeovers of chum salmon nests by coho salmon were passive; female chum salmon had abandoned their nests and died, leaving them prone to dig-up. One female chum salmon was evicted late in the season when the second large pulse of coho salmon entered to spawn, however the chum salmon female had herself dug-up an abandoned coho salmon nest. Intraspecific nest dig-up among chum salmon occurred on 3 of the 65 (4.6%) known chum salmon nests. Intraspecific nest dig-up among coho salmon could

not be verified because coho salmon females were not tagged, however 4 abandoned coho salmon nests were re-occupied during the second arrival pulse of coho salmon and probably were dug-up.

Female chum salmon whose nests experienced dig-up by female coho salmon experienced greater female chum salmon density upon arrival to spawn ( $t=2.47$ , d.f. = 9,  $P=0.03$ ) and constructed their nests in smaller pools ( $t=2.18$ , d.f. = 84,  $P=0.03$ ) than females not experiencing dig-up. There were no significant differences in the incubation characteristics of chum salmon nests that did and did not experience dig-up by coho salmon, however data for only 2 of the dug-up nests exist.

## Discussion

Coho salmon varied more widely in their date of arrival to spawn between two years than did chum salmon and appeared to spawn either before or after major immigrations of chum salmon. In Chapter 2 I demonstrated that female pulse size was a measure of female competition that could affect the porosity of nest site obtained. Small female coho salmon are known to delay stream entry in response to the presence of large female coho salmon (van den Berghe and Gross 1987). Possibly the slight temporal segregation of arrival between chum and coho salmon is a response by the smaller coho salmon to immigration by the larger chum salmon. While in both 1984 and 1985 the two species arrived to spawn at different times, the separation was not

sufficient to prevent re-use of spawning sites and the eggs of both species were subject to dig-up by the other.

Interspecific competition in Walker Creek took the form of passive nest dig-up. Contests for territories between chum and coho salmon were not common, undoubtedly because of temporal and spatial segregation of spawning, however interspecific nest dig-up by coho salmon was more common than by chum salmon and more common than intraspecific nest dig-up among chum salmon. This was a result of two factors, first chum salmon spawned in areas more typical of coho salmon spawning and second, and more importantly, a large number of coho salmon arrived to spawn after the chum salmon.

In chapter 2 I showed how intraspecific breeding competition among chum salmon females could result in the displacement of some individuals to areas of low porosity. Those chum salmon that spawned in coho-type habitat did so when intraspecific competition among chum salmon was intense. This suggests that competition among chum salmon caused displacement to areas more typical of coho salmon spawning where nest dig-up by coho salmon occurred.

In the Tykovskii River (U.S.S.R.) chum and coho salmon spawn in close proximity without interspecific nest dig-up (Smirnov 1976), whereas in other Soviet rivers interspecific nest dig-up does occur between these species (Kuznetsov 1928, Smirnov 1976).

An investigation of interspecific competition between pink and coho salmon in Sashin Creek, Alaska, found that 110 coho



salmon females arrived to spawn after pink salmon in 13000 m<sup>2</sup> of spawning gravel (Crone and Bond 1976). While no nest-dig was observed and the characteristics of pink and coho salmon spawning sites were not compared, Crone and Bond estimated that 2% of the pink salmon eggs could be dug up by spawning coho salmon if they spawned at random among areas of pink salmon spawning and if pink salmon eggs were randomly dispersed. Crone and Bond assumed no nest defense and so do I in applying their method of calculation to the dig-up of chum nests by coho salmon on Walker Creek. The expected dig-up calculated by this method is 21% ( $2.6 \text{ m}^2 \text{ coho}^{-1} \times 20 \text{ coho females arriving after all chum salmon had arrived} \times 246 \text{ m}^{-2} \text{ meters of spawning area used by chum salmon} \times 100$ ) (coho redd size from Crone and Bond (1976)). This estimate is a minimum because I assumed that coho arriving earlier than the last chum salmon dug-up no chum salmon nests. The method of Crone and Bond (1976) overestimates the observed interspecific nest dig-up in the present study by four-fold because it doesn't incorporate salmon behavior; namely, nest defense and spatial segregation of spawning by microhabitat.

In a small area such as Walker Creek the potential for spatial overlap in spawning is considerable, however coho and chum salmon females used different microhabitats for spawning. The selection of particular habitat types was associated with egg survival during incubation. Chum salmon spawned in areas influenced by groundwater with warmer, less oxygenated incubation regimes than did coho salmon. Those chum salmon spawning in cooler, more highly oxygenated incubation regimes,

more typical of areas chosen by spawning coho salmon, experienced high mortality ostensibly because of the low temperatures during early incubation (see discussion in Chapter 2). Coho salmon did not spawn in areas influenced by groundwater and thus its effects on their survival cannot be assessed directly, however temperatures in groundwater would not be harmful as evidenced by the >90% survival of Walker Creek coho salmon eggs incubated ( $\bar{x}=7.5^{\circ}\text{C}$ ) at Mounddale Farms. Apparently chum salmon eggs are less tolerant of cold water incubation than coho salmon eggs, and these differences are not unexpected as such variation exists among chum and pink salmon stocks (Beacham and Murray 1987b).

Interspecific segregation of spawning corresponding with differences in microhabitat parameters was found in a comparison of the spawning microhabitat of brook (Salvelinus fontinalis) and brown trout in Skunk Creek Ontario (Witzel and MacCrimmon 1983). Brook trout used stream headwaters where there was groundwater influence, a higher proportion of fine particles in the substrate, and slow water velocities, while brown trout used the lower reaches of the stream without groundwater influence, with faster water velocities and more highly sorted substrate with a smaller proportion of fine particles (Witzel and MacCrimmon 1983). Brook trout prefer groundwater influenced areas for spawning (Webster and Eiriksdottir 1976) while brown trout avoid them (Hansen 1975), facilitating segregation of spawning.

The time to hatch did not differ between chum and coho salmon eggs at Walker Creek. The time for Walker Creek chum salmon to hatch at 8°C (70 days) reported here agrees well with other data collected on Walker Creek (71 days (Tallman 1986)) and on 7 stocks of Fraser River chum salmon (range 67.4-69.5 days (Beacham and Murray 1985c)). However, coho salmon usually take less time to hatch at 8°C than reported here (69 days). Murray (1980) found 3 Fraser River coho salmon stocks took from 55.8 to 63.2 days while Kubo et al. (1955) found a Japanese stock took 61.5 days to hatch.

Egg mortality by scour in Walker Creek is a significant source of mortality. Scour rates reported here may be overestimates as a result of error in locating nest sites. There was no difference in the rate of scour between the two species which is surprising because coho built their nests in areas of smaller substrate with faster water velocities, areas more likely to be scoured. However, the low number of coho salmon nest sites sampled made detection of significant differences unlikely.

The predicted correlation of substrate size with egg size (Holtby and Healey 1986) and the steepness of the egg size on the body size regression (cf. Fleming and Gross 1987a) was confirmed. However, other factors influence optimal egg size and the correlation between female size and egg size. For example, female competition may vary between streams and between species, and intense female competition will favor a steeper slope in the egg size on body size regression for a given combination of

female size and substrate size. Furthermore, egg size is positively correlated with the length of the developmental period, possibly because more nutrients are needed for the longer period of development (Beacham and Murray 1987a). These influences on egg size must be controlled for in comparisons between populations or species. In the absence of these controls, correlations of substrate size with egg size and the steepness of the egg size on body size regression are insufficient evidence to corroborate the hypothesis that substrate size and female competition determine egg size and the relationship between egg size and body size.

This study has demonstrated that interspecific breeding competition does occur between native salmonids. Although chum salmon use and appear adapted to a different breeding microhabitat than coho salmon, I suggest that intraspecific competition caused an overlap in spawning between the two species, leading to nest dig-up and hence interspecific competition.

## CONCLUSION

Breeding competition among female chum salmon is an important source of mortality. Large and robust females dominate their competitors on the spawning grounds, and natural selection on both body size and morphology by abiotic mortality from gravel scour appears to be influenced by female competition for nest sites.

Female chum salmon growth rate during ocean life is negatively correlated with observed age at maturity, but growth rate from age 3 to age 4 is independent of size. As a result, age at maturity is not consistent with a conditional ESS, assuming ocean mortality is independent of size.

Patterns of female behavior are strongly influenced by competition for nest sites. The distribution of female chum salmon nest sites agrees qualitatively with that predicted if individuals attempt to maximize fitness in a despotic social grouping. The temporal pattern of nest defense suggests that early arriving females defend their nests longer in response to a greater risk of nest dig-up. Arrival date to spawn is influenced by many mortality agents. Female competition and abiotic factors present during the breeding life may play an important role in determining whether natural selection acting on arrival date will result in disruptive or directional selection.

Interspecific breeding competition occurs between female chum and coho salmon, however its intensity is minimized by interspecific segregation of breeding habitat. Chum salmon spawn in areas influenced by warm groundwater, whereas coho salmon spawn in areas influenced by cooler stream water. Cold water incubation is implicated as a source of mortality for chum salmon eggs but not for coho salmon eggs. Habitat selection by the two species is likely a product of natural selection by both female competition and incubation temperature regimes.

#### *Future research*

Future research prospects are considerable. A theoretical treatment of female salmon behaviors such as arrival date to spawn and nest defense might give predictions testable with the large body of data available from Fisheries agencies.

Age at maturity remains an enigma. Investigation of whether adult salmon display both risk-prone and risk-averse foraging strategies in the ocean be worthwhile.

The behavior of female salmon is a function of body size, territorial status, and territorial availability. It may vary not only with female density, but also between populations. Those populations at historically low densities may display different behaviors than those at higher densities. If spawner densities show geographic patterning, then behavior might also show such patterning.

Interspecific competition between Pacific salmon may be more intense in streams with more homogenous habitat, leading to the establishment of a single, dominant species. Consequently there may be a relationship between the heterogeneity of breeding habitat and the diversity of salmon species.

# APPENDIX 1: THE COMPARATIVE ACCURACY OF DIFFERENT METHODS OF ESTIMATING SALMON ESCAPEMENT IN SMALL STREAMS

## Introduction

The spawning escapement of Pacific salmon is a number of considerable importance to both fishery scientists and managers. To the fishery scientist, escapement is a measure of female density and can be used to calculate the intensity of competition, as well as historical trends of abundance. The manager uses escapement data to assess the effect of exploitation on escapement, estimate stock-recruitment curves, forecast future recruitment to the fishery, achieve optimum egg-deposition by controlling the fishery, assess the effects of habitat alteration, and document the timing of spawning runs (Symons and Waldichuk 1984).

The utility of escapement estimates depends on their accuracy and precision in the context of their intended use. Monitoring of long-term trends in escapement requires good precision only, providing that bias is consistent in direction and magnitude. Estimates of long-term productivity from stock and recruitment relationships require accurate data and an estimate of the error in escapement counts (Hilborn and Starr 1984). The consequences of ignoring these considerations can be severe. For example, if a stock-recruitment relationship is used to estimate MSY but the accuracy requirements of the escapement data are not met, then estimates of escapement for MSY can be



seriously negatively biased leading to a loss to the fishery of up to 30% of maximum expected harvest (Walters and Ludwig 1981).

This study compares the accuracy and precision of common methods of estimating escapement. The comparison was made over two years on a small British Columbian stream where ideal enumeration conditions exist. The methods used were mark-recapture, dead pitch, live counts, and the area under the curve (AUC) method. Estimates made by these methods were then compared to a fence count. The effect of error in survey life, a component of the AUC estimate, on error in escapement is assessed and the accuracy of different methods of estimating survey life are compared. The relative accuracy and precision of the various methods were also compared to their relative cost in time and manpower. Finally, recommendations are made regarding the preferred method of estimating escapement in small streams.

### Methods and Materials

Studies were conducted at Walker Creek, B.C., during 1984 and 1985. A fence was constructed at tidewater prior to the beginning of adult salmon migration in both years. Upon arrival at the fence, chum salmon were captured, counted, sexed and then released upstream of the fence. Dates are presented here in units of Julian days. However, because a single season of study can overlap 2 separate years, overlap into the subsequent year is added onto the julian date of the previous year: e.g. January 1 1985 = julian day 366.

The stream residence time of adult chum salmon was determined by tagging individuals with Peterson disc tags and observing them throughout their freshwater lifespan. Tags had unique color or number combinations and this allowed identification of individual fish from a distance. In 1984 20% of the escapement was randomly (using a random numbers table) tagged while and in 1985 100% of the females were tagged whereas none of the males were tagged. Since body size can influence stream residence time (van den Berghe and Gross 1986), an additional random sample of chum salmon was anaesthetized in 2-phenoxyethanol and measured for length ( $\pm 0.5$ cm) and weight ( $\pm 0.05$  kg). To assess differences in stream life between different ages at maturity, a sample of scales was taken from between the lateral line and the dorsal fin and the ages read by the author and the Fish Ageing Unit, Biological Sciences Division, Department of Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, B.C..

Residence time was also estimated with the spawner abundance and death curves through probit analysis (Goldstein 1964). In probit analysis the cumulative abundance and cumulative die-off curves are assigned probit values (normalized values plus a constant) and plotted against log transformed date. Regression lines are then drawn through these data or lines are fitted by eye, and the functions are then compared to yield the mean residence time and the temporal trend in residence time.

Tag loss was assessed by applying a second Peterson disc tag posterior to the dorsal fin of 165 fish, removing the adipose

fin of all tagged fish, and, upon death, examining untagged fish for adipose fins and signs of tagging. Since fish already missing their adipose fins upon entry to the creek would confound estimates of tag loss, chum salmon captured at the fence were examined for the presence of the adipose fin.

Visual counts of adult salmon in Walker Creek were made by foot survey at a mean frequency of 2.5 days. The location, status (alive or dead), sex, and tag number of chum salmon were recorded. The tails of dead fish were cut off to allow the identification of those fish found freshly dead on subsequent surveys. Fish found dead on previous surveys (tails cut off) are referred to as carcasses.

The methods of estimating escapement used in this study were designed either to measure or to minimize variation introduced from a variety of sources. Live counts were made in an upstream direction whereas the dead and carcass counts were made in a downstream direction. Salmon approached while counting upstream tended to turn and swim downstream past the observer. This simplified counting and consequently counts made in an upstream direction were more accurate. Walker Creek was chosen because it was a shallow stream with low turbidity and, thus, bias from these factors was minimized. Officers from the Department of Fisheries and Oceans Canada, who collect the majority of escapement data throughout B.C., also avoid conditions when escapement estimates are likely to be inaccurate by not counting during floods, or by adjusting their estimates to suit the conditions (Cousens et al. 1982, Ames 1984).

The measurement precision of visual counts was measured by repeating a single survey 30 times under standardized conditions. The repetitive surveys were performed by a single observer on the same stretch of stream over a 2 hour period. The use of a single observer may have reduced the variance over that expected if independent counts were made, since the observer knew the previous count and this may have influenced subsequent counts. The variation in live counts introduced by observer bias was assessed by having observers perform counts simultaneously. Variation in live counts was reduced by ensuring that counts were made between the hours of 1000 and 1400 and then only when visibility through stream water was greater than 1.5 meters.

The duration of freshwater life of adult salmon is referred to as residence time (Neilson and Geen 1981), stream life (Helle 1979, Ames 1984), turnover time (Cousens et al. 1982), average life expectancy (Gangmark and Fulton 1952), average lifespan (Killick 1955) and breeding life (van den Berghe and Gross 1986). In the present study residence time was determined from the repeated observation of individually tagged chum salmon. Residence time was calculated as the time elapsed from when a fish was passed over the fence until it was recovered dead, corrected for the time elapsed between surveys. Survey life, the period of time fish are visible for counting, is the statistic of interest when estimating escapements. It has also been called residence time at the redd site (Neilson and Geen 1981) and erroneously referred to as redd life (Helle 1979), which is actually the length of time a redd is visible to an observer

(see Newman 1984). The true survey life cannot be measured, only estimated by the residence time minus some factor accounting for when the salmon are not visible while holding out of view in pools prior to or after spawning. Fish were visible immediately after release upstream of the fence, consequently survey life was the time elapsed from the time passed over the fence until its final live observation. Since foot surveys were made every 2.5 days, residence time and survey life measurement error was  $\pm 1.25$  days. Fish that lost tags or that appeared to have been dead a long time when found were not included in the calculation of residence time.

Since sex-specific survey life measures may be used in estimates of escapement (Ames 1984) and the method of doing this is to weight sex-specific averages by sex ratio, sex ratios were determined by three methods to compare their accuracy. The sex of all chum salmon was recorded as they were passed over the fence, as they were recovered dead during the foot surveys, and as carcasses washed downstream to the fence.

The AUC estimate was calculated following Cousens et al. (1982) as:

$$TS = AUC / SL$$

where TS = total number of spawners

AUC = integral of spawner abundance curve

SL = mean survey life

The method of integration used here is by parts.

Escapement estimates by the mark-recapture technique are calculated as follows:

$$N=M*C/R$$

where N= estimate of the total population, N  
M= original number of individuals marked  
C= number of individuals examined for marks  
R= number of marked individuals recovered.

## Results

In 1984 1231 chum salmon were captured at the fence while in 1985 only 254 were captured. Figures A.1 and A.2 show the cumulative arrival curves, daily live, dead, and carcass counts for 1984 and 1985 respectively. No counts of daily dead were made in 1985, while in 1984 carcass counts were not made after December 31 (Julian day 365) when a snowfall prevented observation.

Figure A.3 illustrates a histogram of repetitive counts made under standardized conditions ( $\bar{x} = 95$ ,  $\sigma=9.0$ ,  $n=28$ , 95% C.L.=  $92 < \bar{x} < 98$ ). Proportionally the confidence limits are  $\pm 3.7\%$ .

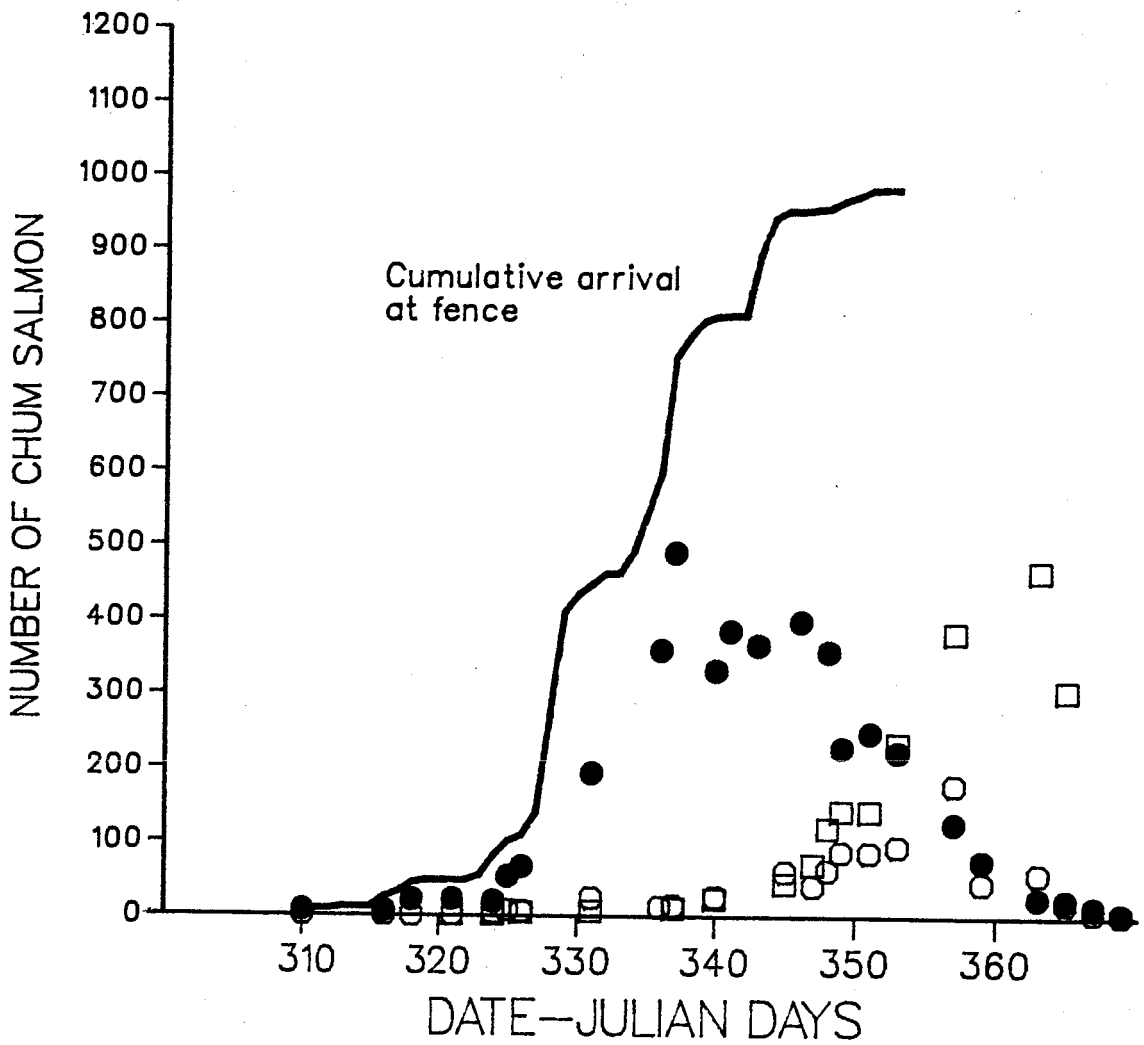
Visual counts made by two experienced observers were used in escapement estimates. On two occasions these observers made simultaneous counts and these differed by only 0.5% and 5%, consequently observer effects were ignored and visual counts by these observers were pooled (in the case of simultaneous counts means were calculated).

Tag loss was determined for both tag locations by examining all fish during the dead recovery. Tags applied anterior to the dorsal fin were lost at a rate of 4% while tags applied posterior to the dorsal fin were lost at a rate of 7.9%. The fact that only 19.0% of recovered dead fish had tags while 20.0% were originally tagged suggests a tag loss of 5%.

The influence of tagging on observability can be assessed by comparing the observed proportion of tags among live fish to the

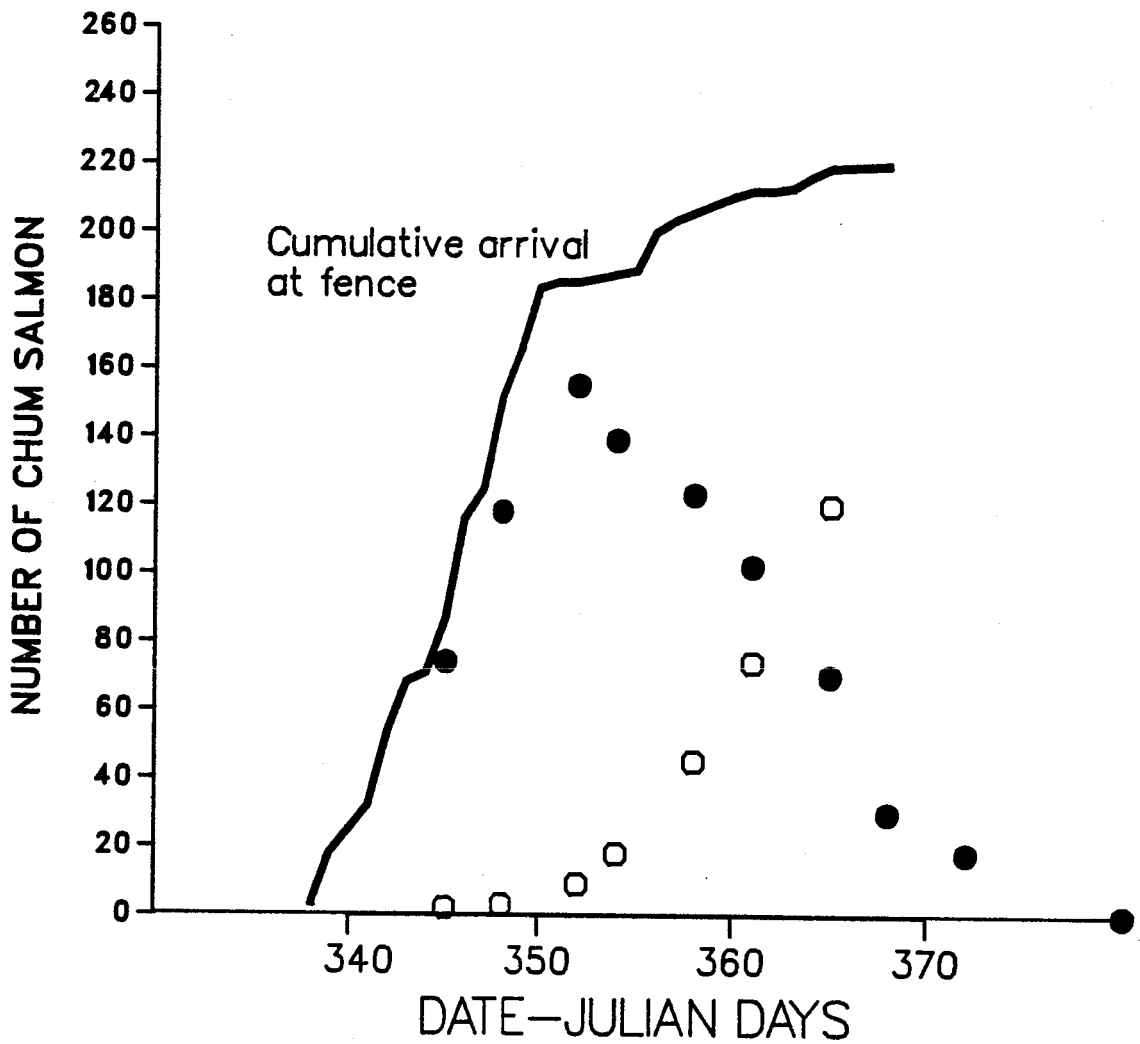
Figure A.1: Cumulative arrival, daily live, dead and carcass counts of chum salmon in Walker Creek, 1984.





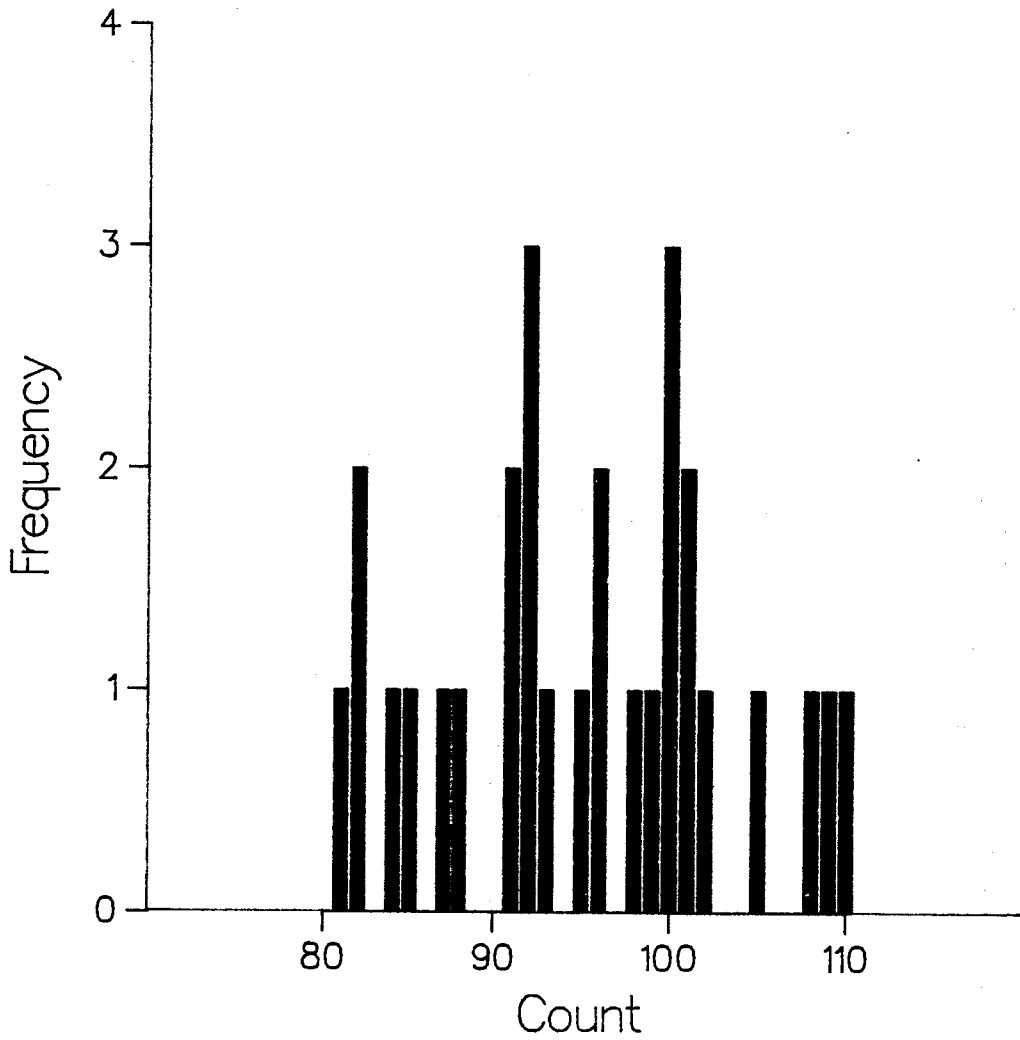
- Legend**
- live count
  - dead count
  - carcasses

Figure A.2: Cumulative arrival, daily live and carcass counts of chum salmon in Walker Creek, 1985.



**Legend**  
 ● live count  
 □ carcasses

Figure A.3: Histogram of chum salmon count frequencies in a controlled trial.



proportion tagged at the fence (20%) and the proportion recovered from dead fish. In 1984 the average live count was 167 of which an average of 36 (21.7%) were tagged. Dead pitching recovered 839 dead chum salmon of which 159 (19%) were tagged. Correcting for 4% tag loss gives 22.4% observed tagged and 19.7% recovered tagged, suggesting that tagged fish were slightly, although not significantly, more visible than untagged fish.

The sex ratio in 1984 determined by examining each fish at the fence was 1.89 males to every female (n=1231). The sex ratio as determined from carcasses drifting into the fence was 1.33 males to every female (n=21). This was significantly different from the sex ratio determined from those fish arriving at the fence (12 males in 21 trials with  $P(\text{male}) = 0.66$ , binomial prob = 0.05). The sex ratio as determined from the recovery of tagged dead chum salmon during dead pitching was 1.84 males to every female (n=159).

#### *Expected versus observed live counts*

The expected number of live fish on a survey is calculated as the cumulative fence catch minus the cumulative number of dead, corrected for the rate of carcass loss. The rate of carcass loss is calculated using data on the number of fresh dead and carcasses present on two consecutive surveys. Rate of carcass loss is calculated as:

$$\Delta C = \text{carcasses}_t * (\text{fresh dead}_{t-1} + \text{carcasses}_{t-1})^{-1}.$$

Figure A.4 illustrates the number of carcasses recovered as a function of the total number of dead on the previous survey

(adjusted R square =0.88, F=139, d.f.=17, P<0.0001). The residuals of this regression were not significantly correlated with survey date, the number of carcasses on the previous survey, or the time elapsed between surveys. The number of fresh dead found on a survey can be corrected for the rate of loss by the formula;

$$\text{corrected dead} = \Delta C * (\text{number dead}),$$

where  $\Delta C$  is the rate of carcass loss, specific to the survey interval.

The sum of corrected dead was 1112, 119 (9.7%) less than the total escapement. This difference may be attributable to the poaching of live fish, predation, and the entrapment of dead fish within debris where they were invisible to observers. Sixty-eight percent of the total escapement was recovered during the dead pitch and carcass loss accounted for an additional 22% of the total escapement.

Figure A.5 illustrates the difference between observed and expected live counts. The area under the observed curve is 9426 chum days, while the area under the expected curve is 20987 chum days, thus visual counts were biased by -55%. In 1986 the integral of the spawner curve was 2651 days but expected counts could not be calculated because no estimate of the rate of carcass loss was made.

Figure A.4: Carcasses recovered as a function of the number dead on the previous survey.



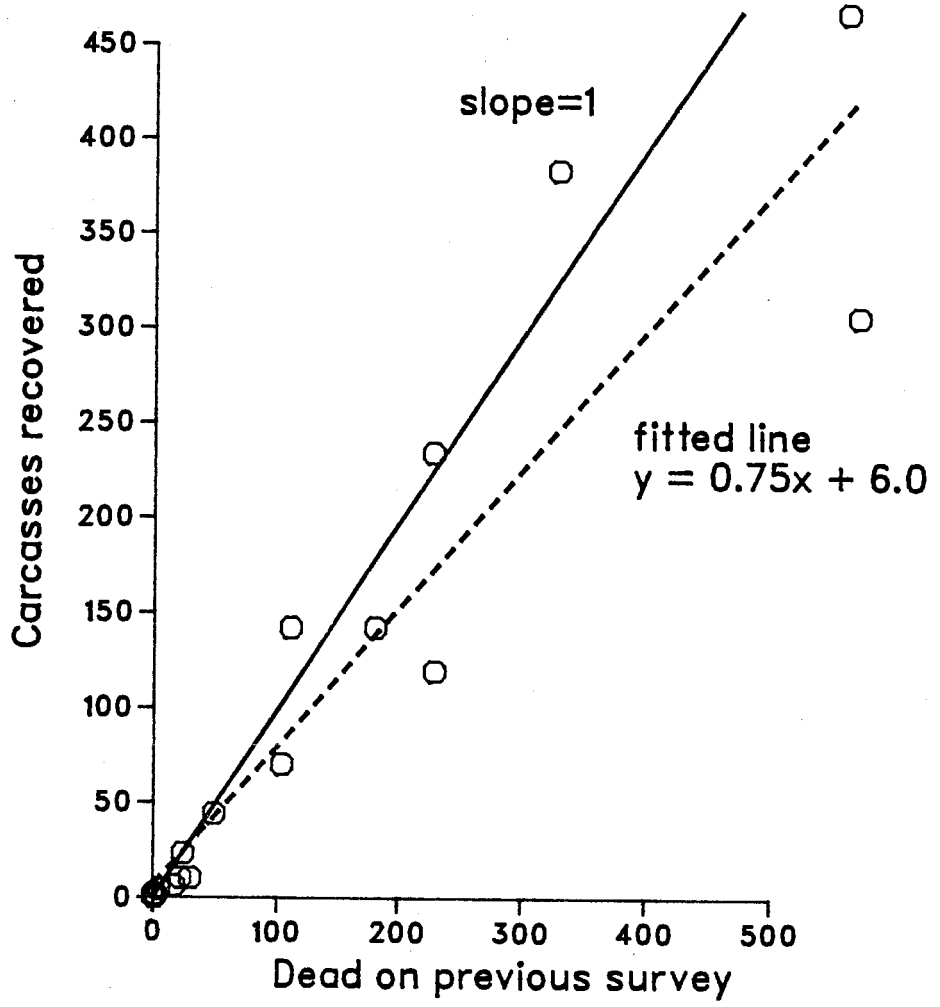
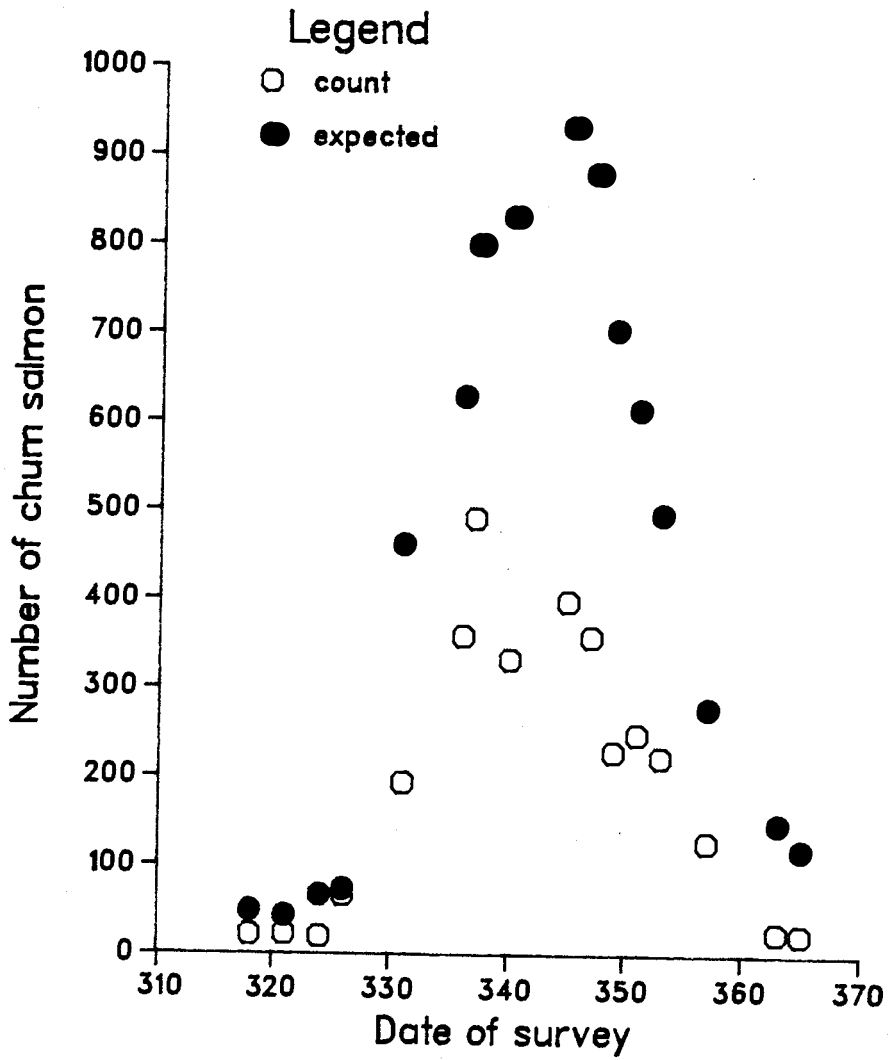


Figure A.5: Expected versus observed counts of chum salmon in Walker Creek during 1984.



## *Residence time measurements*

Residence time during 1984 was determined for only 157 of the 256 (61.3%) chum salmon tagged because I excluded from analysis fish that were not recovered dead, fish that lost tags, and those I suspected had been dead for a period greater than the interval between counts. The average residence time for both sexes was 17.5 days ( $\sigma=4.96$ ,  $n=157$ , range 4.5-30.5) as determined from dead recovery, while survey life was 12.7 ( $\sigma=5.61$ ,  $n=95$ ) as determined from the last live observation (Table A.1). The minimum residence times represent fish that were killed by predators.

Tag loss was considered to have no effect on residence time or survey life determination because of its low incidence. Tag loss is likely correlated with residence time and could bias downward the residence time estimate in a situation in which tag loss was higher because long-lived fish are more likely to lose their tags and not be included in the residence time sample.

Male chum salmon had significantly longer residence times than females (18.0 versus 16.7 days) during 1984 (Mann-whitney U test:  $Z=2.31$ ,  $d.f.=156$ ,  $P=0.02$ ), and female chum salmon differed significantly in residence time between years ( $T=2.58$ ,  $d.f.=180$ ,  $P=0.01$ ) (Table A.1). Females and males did not differ significantly in survey life in 1984, in fact females had a longer survey life, a difference opposite that detected for residence time. This suggests that male and female chum salmon differ in their behavior near the end of their adult freshwater

life. There were no significant differences in residence time between fish of different ages, body weights, or fork lengths. There was a significant decrease in residence time with season among both sexes in 1984, and among females in 1985 (Table A.1).

In 1985 male residence time was not measured, but was estimated from female residence time \* 1.078 (the relative value in 1984), to give a mean male residence time estimate of 16.3, and a population mean residence time estimate of 15.8. In 1984 male survey life = 0.925 \* female survey life. Applying this correction factor in 1985 gives a male survey life estimate of 12.7 and a population mean survey life estimate of 13.2.

In 1984 residence time was 38% higher than survey life (Table A.1). In 1985 residence time was 10% higher than survey life. The frequency of observations was more frequent in 1985 than in 1984, suggesting a negative correlation between frequency survey and the difference between residence time and survey life estimates.

When recovered dead, salmon frequently were missing for one or more survey periods. This may be a result of their tendency to hide under banks or in debris when nearing death, becoming visible only when they die and are moved by the current into view of the observer. Residence time must be corrected for those periods when fish are not visible for counting if it is to be an accurate estimate of the period fish were visible for counting. Consequently survey life is merely residence time corrected so that the period when fish are not visible is excluded.

Table A.1:

Walker Creek chum salmon residence time and survey life measures.

Year	Females			Males			Total		
	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n	$\bar{x}$	$\sigma$	n
<b>Residence time</b>									
1984	16.7	5.56	54	18.0	4.59	103	17.5	4.96	159
1985	15.2	6.20	127	16.3 <sup>1</sup>	-	-	15.8 <sup>1</sup>	-	-
<b>Survey life</b>									
1984	13.3	5.06	38	12.3	5.96	57	12.7	5.61	95
1985	13.8	7.44	118	12.7 <sup>1</sup>	-	-	13.2 <sup>1</sup>	-	-

**Temporal trends in residence time**

Males 1984	$y = -.16x + 71.6$	$F=5.77, P=.02,$	$d.f. =101$
Females 1984	$y = -.38x + 143,$	$F=12.8, P=.001,$	$d.f. =52$
Females 1985	$y = -.36x + 352,$	$F=11.8, P=.001,$	$d.f. =58$

<sup>1</sup> Estimates (see text)

A second method of measuring the residence time of adult salmon is to compare the peaks of daily live and dead counts. The time elapsed between the modes of immigration and die-off is the residence time. Survey life cannot be calculated by this method unless a correction factor subtracting the time between the last live observation and death is applied to the dead recovery curve. This correction factor must be determined from the observation of individually tagged fish, consequently only residence time, not survey life, can be calculated from plots of live and dead count data. The bias in the residence time calculated by this method is reported with respect to the residence time determined from observation until dead recovery. In 1984 the residence time estimates from this method are; first peak 12 days, second peak 11 days (Figure A.1), an average bias of -9.4%. In 1985 the estimate made by this method was 13 days, a bias of -18%. The reason that the 1985 estimate is less accurate is that it is based on the carcass recovery data, rather than the daily dead data, which were not collected in 1985. Carcass recovery was not performed for the entire season in 1985, consequently the true peak carcass count may be later than observed and because of this the 1985 residence time estimate will be negatively biased.

The third method of residence time determination is to perform probit analysis using the spawner abundance and die-off cumulative curves. This method has been used extensively to generate residence time measures which are then used to calculate escapement estimates using the AUC method (Hickey and

Lister 1981, Olmsted et al. 1981, Whelen and Morgan 1984 and others).

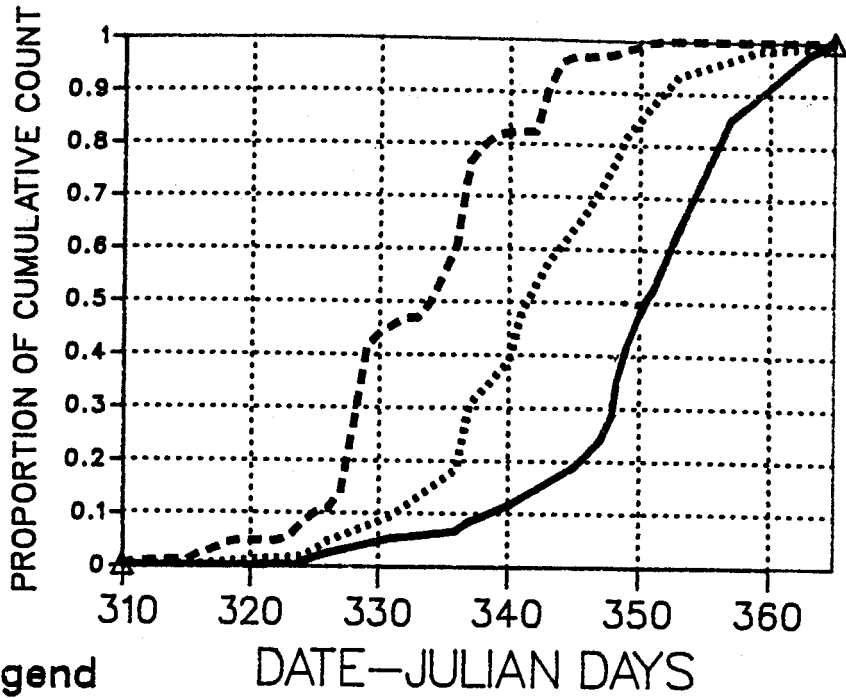
The common procedure for estimating residence time from cumulative abundance and die-off curves is to plot the cumulative curves against date and to measure from the plot the difference in date between equivalent points of the cumulative curves. These equivalent points are usually taken at 0.1, 0.5, and 0.9 of the cumulative curves and differences in residence time between these values are frequently interpreted as evidence of a temporal trend in residence time (Hickey and Lister 1981, Olmsted et al. 1981, Whelen and Morgan 1984 and others).

Usually cumulative arrival data are unavailable and fish abundance is determined using the cumulative visual count curve. This introduces a serious negative bias into the residence time estimate as illustrated in Figure A.6. From the cumulative arrival curve the estimates at 0.1, 0.5, and 0.9 are for 1984; 14.0, 15.9, and 16.4 days, and for 1985; 10.5, 14.0, and 15.4 days. From the cumulative spawner count curve the estimates at 0.1, 0.5, and 0.9 are 6.5, 8.0, and 7.5 days for 1984, and 7.5, 7.8, and 6.0 days for 1985. Assuming that the date of arrival and death are normally distributed, the difference in days between 50% equivalent points will equal the average residence time. Based on these averages, the bias in residence time estimates from cumulative arrival data are +25% and +10% for 1984 and 1985 respectively. The bias in residence time estimates from cumulative visual count data are -37% and -58% for 1984 and 1985 respectively. Although residence time calculated from



Figure A.6: Cumulative curves of chum salmon arrival, visual counts, and death at Walker Creek during 1984 and 1985.

1984



Legend

- arrival
- count
- dead

1985

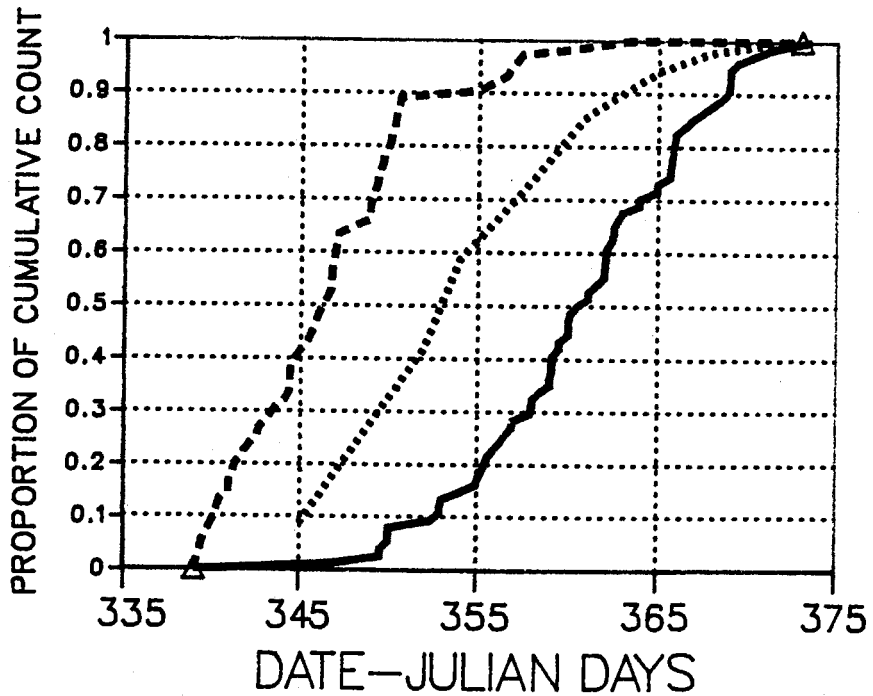
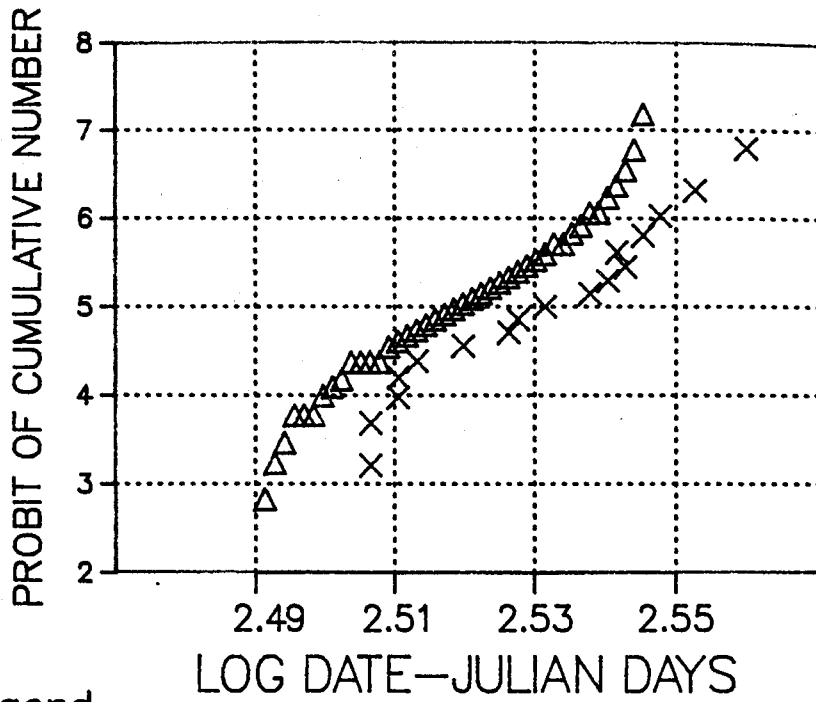


Figure A.7: Probit analysis of cumulative arrival and death curves from Walker Creek chum salmon, 1984 and 1985.

1984



**Legend**

- △ arrival
- × death

1985

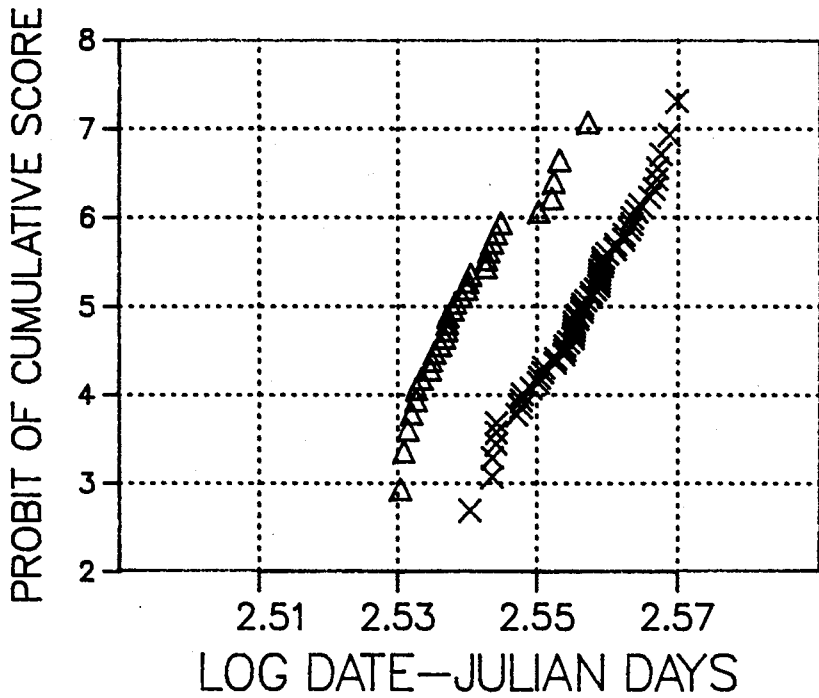
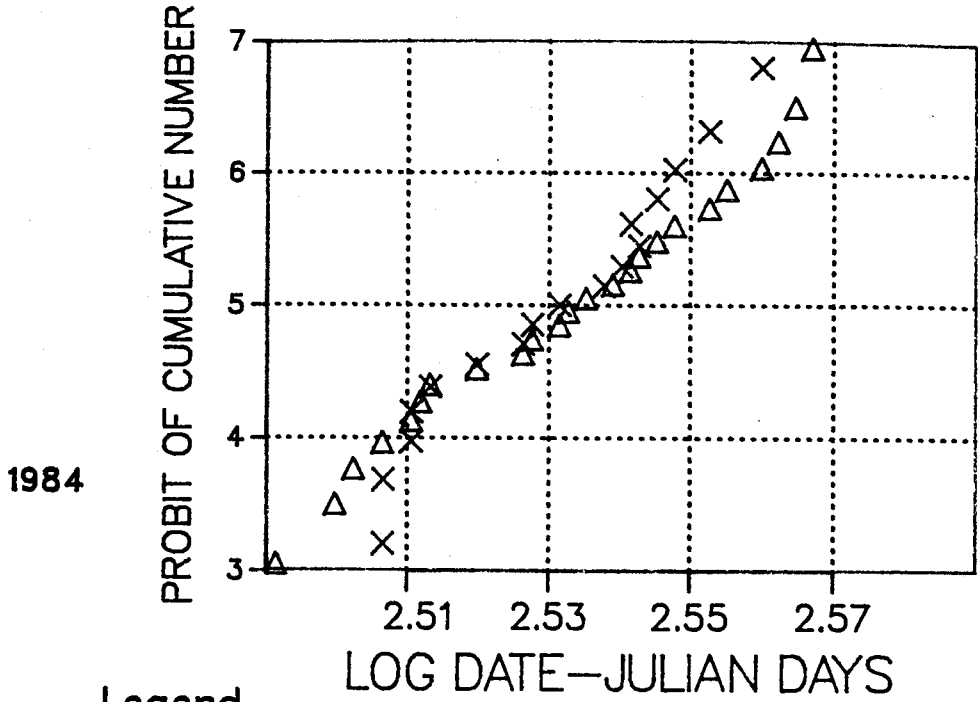
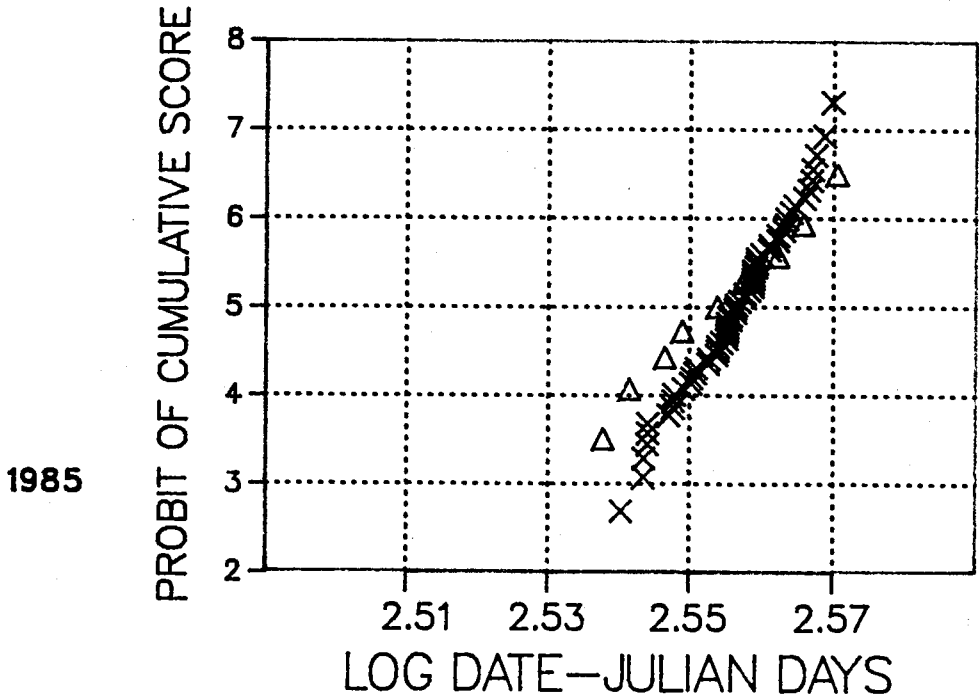


Figure A.8: Probit analysis of cumulative visual count and death curves from Walker Creek chum salmon, 1984 and 1985.



**Legend**  
 △ count  
 X death



cumulative visual count data is more biased than that calculated from cumulative arrival data, the former is closer to the survey life than the latter because it is negatively, rather than positively, biased. This negative bias compensates for the positive bias of residence time as a measure of true survey life.

No temporal trend in residence time was detected by any of these estimates in contrast to the negative correlation detected in data obtained from observing individually tagged fish. This is partially a result of the intersection of the cumulative abundance and death curves at proportions of 0.0 and 1.0, which ensures that residence time calculated by this method decreases at the beginning and end of the season. A more correct procedure for estimating survey life trends from cumulative abundance and die-off curves is to perform a probit analysis. The probit analysis of the untransformed data presented in Figure A.6 are presented in Figures A.7 (arrival data) and A.8 (visual count data). The data in Figure A.7 are curvilinear in form, and a Shapiro-Wilk test (Shapiro and Wilk 1965) for normality found significant non-normality for the 1984 data and the 1985 arrival data. As a result, predicting the trend in residence time from probit analysis is inappropriate since it assumes normality. In both 1984 and 1985 the two cumulative functions tend to diverge, a result opposite that expected if residence time decreases through the season. The cumulative count data in Figure A.8 also are non-normal and while the two cumulative functions do intersect, suggesting negative residence during the latter part

of the season, the functions also converge, the result expected if residence time decreases through the season.

Residence time varies greatly among species and populations of Pacific salmon (Table A.2). Population means vary from 5.0 to 28.9 between species and from 6.2 to 18.9 between populations within species. While the variation does, to some extent, reflect differences in methodology, obviously using non-species or non-population specific residence time estimates in AUC calculations could result in serious bias.

#### *AUC estimates*

The AUC estimate using the integral of the live count curve and the survey life estimate gives escapement estimates of 742 and 201 for 1984 and 1985 respectively. The same calculation using the residence time estimate gives an escapement estimate of 525 and 182 in 1984 and 1985 respectively. Use of the residence time estimate from the cumulative visual count and death curves give escapement estimates of 1178 and 340 respectively during 1984 and 1985.

Error in survey life has an asymmetrical and non-linear effect on the error in escapement estimate. When survey life underestimates the true survey life, error in escapement increases at an increasing rate (Figure A.9). The data in Figure A.9 are from simulations of the AUC estimate iterated over a range of errors in survey life and live counts, the two components of the AUC estimate. For example, using an integral spawner curve of 9426 days and a true survey life of 16 days, a



Table A.2:  
Pacific salmon stream residence times.

<b>Coho salmon</b>				
Sashin Cr.	1965	13.0 <sup>1</sup>	6-21	Crone and Bond 1977
	1967	11.0 <sup>1</sup>	3-24	"
	1967	9.0 <sup>2</sup>		"
Funny Cr.	1965&67	5.0		"
Spring Cr.	1951	11.3		Willis 1952
Deer Creek Jr.	1982-83	9.1		van den Berghe & Gross 1986
<b>Sockeye salmon</b>				
Fulton R.	1972	9.4		Tautz 1977
Forfar Cr.	1952	12.4		Killick 1955
Adams R.	1954	18.9		"
Weaver Cr.	1941	9.0		Schaefer 1951
Weaver Cr.	1940	8.7		"
Kvichak	1959	7.8		Hartman 1959 in Foerster
Hansen Cr.	1949	6.2		Mathisen 1955
Pick Cr.	1949	34.4 <sup>3</sup>		"
Karluk Lk.	1952	7.0		Gangmark and Fulton 1952
USSR	1928	15.0		Kuznetsov 1928
<b>Chinook salmon</b>				
Nechako R.	1980	14.5 <sup>1</sup>		Neilson and Banford 1983
Morice R.	1979	12.0 <sup>1</sup>		Neilson and Geen 1981
Mussel Creek	1983	25.0		Whelen and Morgan 1984
<b>Pink salmon</b>				
Southeast Alaska		5.6-31.5		Dangel and Jones 1987
Seton Cr.	1957	14.0		Ward 1959
Fraser R.	1957	25.3		"
Thompson R.	1957	16.5		"
Harrison R.	1957	21.5		"
Chilliwack R	1957	28.9		"
Ahnuhati River	1983	17.6 <sup>4</sup>		Whelen and Morgan 1984
Tom Browne Cr.	1983	24.0 <sup>4</sup>		"

<sup>1</sup> females only

<sup>2</sup> males only

<sup>3</sup> fish penned during freshwater life

<sup>4</sup> determined from cumulative stream count data

Table A.2 cont.:

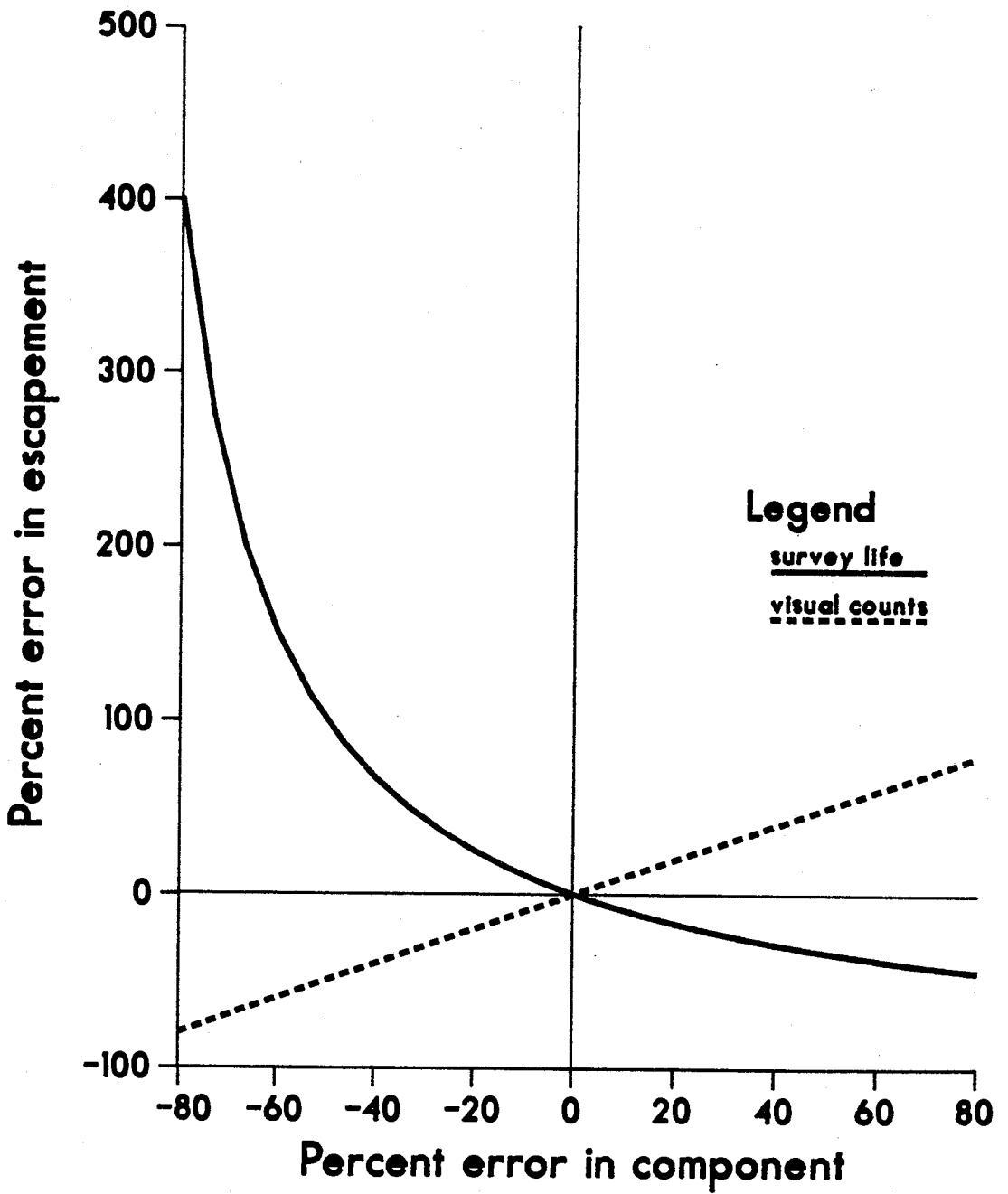
**Chum salmon**

Big Qualicum	1963	11.1	Lister and Harvey 1969
Walker Creek	1984	17.5	present study
Walker Creek	1985	13.2 <sup>5</sup>	"
Minter Creek	1952	10.5	Ames 1984
Perkins Creek	1974	9.5	"
Johns Creek	1977	10.1	"
Yelm Creek	1976-81	9.7	"
Big Beef Cr.	1970	15.1 <sup>3</sup>	Schroder 1973
	1971	13.8 <sup>3</sup>	Schroder 1973
Olsen Cr.	1967	8.5	Helle 1979
Olsen Cr.	1968	11.4	Helle 1979

<sup>3</sup> fish penned during freshwater life

<sup>5</sup> estimate based on females only (see results)

Figure A.9: Error (%) and bias direction in the area under the curve escapement estimate as a function of percent error in salmon survey life and visual counts.



survey life estimate of 10 days (-37.5% error), results in an escapement error of +60%. AUC estimates are more robust against overestimates of survey life. For example, a survey life error of +20% results in an escapement error of -17%, while a survey life error of +100% results in a -50% error in escapement. In contrast, error in visual counts has a linear effect on error in escapement (Figure A.9).

### *Mark-recapture*

During the mark-recapture estimate for Walker Creek in 1984, 246 fish were tagged and 839 were recovered, of which 159 were tagged. Thus the mark recapture estimate is (see methods for symbol definitions):

$$N = (246 \times 39) / 159 = 1298.$$

If  $M \times C > 4N$  then statistical bias will be  $< 2\%$ , which is true in the present case as  $M \times C = 206394 > 4 \times N = 4924$ . The adjusted Peterson estimate ( $N = (M+1) \times (C+1) \times (R+1)^{-1}$ ) is an unbiased estimator of  $N$  and used only if  $M+C > N$ . In the present case  $M+C = 1085 < N = 1231$ , thus the adjusted Petersen estimate is inappropriate. From Ricker (1975) we find that if  $500 < C < 1000$  and if  $R \times C^{-1} \gg 0.075$ , then the sampling distribution of the estimate will approximate the normal distribution. Our estimate meets the above criteria and so from Ricker (1975 (formula

#3.8)) we calculate 95% confidence limits as follows:

$$\text{C.I.} = N * 1.96 * [(C-R) * ((C+1)(R+2))^{-1}]^{0.5} * 2$$

$$= 342$$

Therefore our Petersen mark-recapture estimate with confidence limits is:

$$N = 1298 \pm 171$$

$$(1127 < N < 1469).$$

A population estimate from mark-recapture data can be calculated using a non-random system of tag application. Although the tags were applied in a random fashion, we can assess the effects of applying them non-randomly by defining our initial capture sample (C) as that which occurred within a specified time period of short duration. Note that tag retrieval remains random, thus the estimate should remain unbiased. Utilizing recaptures of fish tagged only on Julian days 328 and 329 and using calculation methods as described above we get the

following estimates and confidence limits.

$$N = 1147 \pm 638$$

$$(855 < N < 1493)$$

Note that neither that random or non-random estimate accounts for tag loss and yet both encompass the actual escapement within their confidence limits, although the non-random estimate is 88.4% of the random estimate.

### *Summary of results*

Table A.3 lists the estimates and 95% confidence limits where applicable. The accuracy of escapement estimates relative to the fence counts varies between years but is, in descending order of accuracy: mark-recapture, dead pitch + drifting carcasses, dead pitch alone, AUC estimates (as a group), sum of 2 counts at intervals roughly equal to residence time, live + dead at peak abundance, single live plus dead after immigration ends, and single live count at peak.

Table A.3:

Comparison of escapement estimates.

	1984		1985	
Fence	1231		254	
FOOT SURVEY	Estimate	error <sup>1</sup>	Estimate	error <sup>1</sup>
Single live count at peak spawner abundance	491	-60%	155	-39%
Single live + dead at peak spawner abundance	515	-58%	164	-35%
Single live + dead after immigration ends	456	-63%	190	-25%
Sum of two or more live counts made at intervals equal to residence time	525	-57%	182	-28%
AUC <sup>2</sup>	742	-40%	201	-21%
AUC <sup>3</sup>	1178	-4%	340	+34%
AUC <sup>4</sup>	592	-52%	189	-25%
AUC <sup>5</sup>	525	-57%	182	-28%
Dead pitch	839	-32%	NA	
Dead pitch plus drifting carcass recovery.	901	-27%	NA	
MARK-RECAPTURE				
Random	1298	±171 +5%	NA	
Non-random	1174	±319 -5%	NA	

- <sup>1</sup> Error with respect to the fence count
- <sup>2</sup> Survey life determined by observation
- <sup>3</sup> Survey life calculated from cumulative  
visual live count and death curves
- <sup>4</sup> Survey life calculated from cumulative  
arrival and death curves
- <sup>5</sup> Residence time in place of survey life



## Discussion

Methods of estimating salmon escapement applied here differed greatly in their accuracy. Many of these estimates are based on visual counts and are dependent on their accuracy and precision. The coefficient of variation of visual counts was .095 which is similar to that reported in a small clear Alaskan stream for pink salmon counts ( $x=201$ , C.V. = .091, Sheridan 1962). Differences between observers in visual counts were not detected in the present study in agreement with Sheridan (1962) who found observer differences did not explain significant variation in counts.

In the present study, the single live count at peak abundance was the poorest estimate for two reasons. First, visual counts underestimate escapement and secondly the spawning run was longer in duration than residence time and thus all the spawners did not inhabit the spawning grounds simultaneously. Consequently basing the escapement estimate on a single count limits the number of fish that can possibly be counted to a number less than that of the actual escapement. Furthermore information about when to make counts to minimize bias is unlikely to exist. Estimates using the sum of two counts are poor; even in the best scenario this estimate had a bias of -50%.

Cousens et al. (1982) report that visual counts are often 30 to 50% of the actual escapement. Solazzi (1984) found visual counts of chum salmon were 85% of the true escapement as

determined by electroshocking, while Shardlow et al. (1987) found that the probability of seeing a chinook salmon during a foot survey was only 0.28. The present study was performed on a stream where ideal counting conditions existed: low discharge, no turbidity, and shallow. Nevertheless, the integral of counts was only 46% of expected. While the accuracy of visual counts is low, the precision of measurement is high (95% C.L.  $\pm 3.7\%$ ) when compared to that of other methods (Cousens et al. 1982, Simpson 1984).

The most accurate estimate employing single as opposed to multiple visual counts was the single live plus dead at peak abundance in 1984 and the single live plus dead after immigration ended in 1985. All escapement estimates based on visual counts were more accurate in 1985 than in 1984. This is likely because less predation occurred in 1985 than in 1984, because escapement was smaller, making enumeration easier, and because average water discharge was less in 1985 ( $0.034 \text{ m}^3\text{sec}^{-1}$ ) than in 1984 ( $0.28 \text{ m}^3\text{sec}^{-1}$ ), lowering water depths and making fish more visible. In both years turbidity was negligible and conditions were ideal for observing fish, nevertheless, the difference in count accuracy between years suggests annual variation in fish observability, further suggesting that stream counts are not comparable between years even in ideal streams.

On Walker Creek the deadpitch estimate of escapement was more accurate than methods employing visual counts. A reason for the high accuracy of the dead pitch was that carcass wash-out was infrequent (6.9% of the dead pitch), as expected on a stream

as small as Walker Creek. In addition to loss through wash-out, carcasses decompose and are eaten. A correction for total carcass loss increased the dead pitch estimate by 32.5%, however 9.8% of the fence count was still not accounted for. Possibly these fish were removed by predators or hidden after death by debris.

Survey life was measured by observing tagged fish throughout their stream life. Residence time as determined by dead recovery was within 10% of survey life in 1985. Survey life measured in 1984 was less accurate because of the low frequency of observation. This suggests that in studies using dead recovery to estimate residence time, fish should be inspected to ensure that they died recently and surveys should be made frequently. In other rivers, where salmon hold in deep pools where they are not visible prior to spawning (cf. Neilson and Geen 1981), residence time may not always be as accurate a measure of survey life as reported here, where salmon were visible immediately after release upstream of the fence.

Cumulative abundance and death curves cannot accurately measure survey life because survey life is correctly calculated to the last live observation, not to the time of death. This error can be corrected if visual counts include the number of dead since the last survey because then the integral of the spawner abundance curve would include the additional time until dead recovery.

A significant conclusion of this study is that cumulative arrival and spawner count curves are not equivalent. Estimates of residence time from the comparison of cumulative abundance and death curves are reasonably accurate only if they use arrival data. Estimates of residence time calculated from cumulative visual count data are seriously negatively biased and should not be used. In the present study, their -37% to -58% bias would, in theory, result in a +60 to +140% error in escapement because of the asymmetric, non-linear relationship between survey life error and escapement error. Probit analyses of cumulative abundance and death data are also only appropriate with arrival data, and these data must be normally distributed if temporal patterns in residence time are to be detected. While arrival data can be used to generate residence time estimates, this is rarely practical since it requires the trapping of upstream migrants, an activity which allows the tagging of individual fish, which in turn allows residence time to be determined by direct observation.

The AUC estimate calculated using survey life determined from observation gave a poor estimate of escapement (-40% and -28% bias for 1984 and 1985 respectively). This is primarily a result of the negative bias of visual count data. The integral of the spawner abundance curve was biased by -55% in 1984 and, given the linear relationship between visual count error and escapement error, we expect the AUC estimate to be equally biased. However, the 1984 AUC estimate is biased by only -40%, suggesting that there may be error in the calculation of the

expected counts. A possible cause of this error is that fish accounted for by the carcass loss correction were removed by predators prior to counting.

An interesting finding of this study is that both visual counts and survey life estimates determined from cumulative spawner counts tend to be negatively biased. As a result, such AUC escapement estimates are accurate because errors in their components tend to cancel out. This is not justification for using cumulative spawner counts to determine survey life, but rather a fortunate outcome.

The survey life estimate is important in determining the accuracy of AUC estimates. Error in escapement estimates calculated using the AUC method vary in an asymmetric non-linear fashion with error in survey life. Consequently it is important to avoid negatively biased survey life estimates.

Residence time differences between sexes existed, however similar differences in survey life did not. When sex ratio is skewed, AUC calculations using population mean residence time measures could be biased. Use of mean female residence time instead of the population mean residence time to calculate the 1984 AUC estimate would have resulted in an additional 7% error in escapement. The method of determining sex ratio is important: carcasses have differential drift rates and in the present study estimates based on drifting carcasses underestimate the proportion of males, as has been previously found (Cousens et al. 1982).

More significant than the error from variation between sexes is the effect of interannual variation in mean residence time. Residence time differed between years by only 1.5 days (females in 1984 compared to 1985), however using the 1984 residence time estimate in the 1985 AUC calculation results in an escapement error of 10%. Population mean residence time/survey life comparisons between years are not made here because male residence time/survey life data were not measured in 1985 but extrapolated from the female residence time data corrected for sex differences found in 1984.

Residence time did not differ between fish of different sizes, in agreement with Schroder (1973) but in contrast to van den Berghe and Gross (1986). Temporal trends in residence time as found here can affect escapement estimates as discussed by Neilson and Geen (1981).

Wide variation in mean residence time exists between species and populations of Pacific salmon. The mean from this study (17.5) is high compared to most estimates from the literature for chum salmon. While the accuracy of AUC estimates can reach  $\pm$  10 to 15% of weir counts (Flint pers. comm. cited in Cousens et al. 1982), the effect of error in survey life on escapement estimates suggests that survey life should be calculated every year. Even when accurate estimates of survey life are available, the inaccuracy of visual counts ensures a negative bias of escapement and a resultant loss to the fishery. Guessing high when estimating survey life will reduce error compared to guessing low, but will negatively bias the escapement estimate,

possibly compounding the negative bias of visual counts.

The mark-recapture estimate was an accurate estimate of escapement, likely because mark-recapture estimates are insensitive to mortality providing it is the same for tagged and untagged fish. The precision of this estimate is dependent on the initial number tagged and number of tags recovered. The present study was performed under ideal conditions. There was random tag application and retrieval, infrequent tag loss and a high percentage of tags were recovered. Furthermore there was no differential emigration of tagged and untagged fish as verified by the similarity of the proportions of fish tagged and recovered tagged.

Generally mark-recapture methods overestimate actual escapement (Simpson 1984). This is due primarily to tag loss and a higher mortality of tagged fish. Mark-recapture techniques cannot be relied upon to be precise and a large variation has been found between tests that were near-replicates (Simpson 1984).

The dead pitch method of estimating escapement, while the most accurate of those methods employing simple counts, was far less accurate than mark-recapture estimates. However, the mark-recapture experiment was far more labour and time intensive (time spent capturing and tagging fish), thus in small streams where carcass wash-out is expected to be minimal, a dead pitch is recommended. No estimates of the precision of the dead pitch were made, although high precision is expected on Walker Creek.

Analysis and interpretation of data on the precision and accuracy of escapement estimates requires continued research. Measurement of the accuracy and precision of counts under a wide range of population sizes and stream channel configurations would show how fish density affected count accuracy and provide correction factors. Data on carcass loss rates from streams larger than Walker Creek would expand the utility of the live plus dead counts and allow the application of carcass loss rates to other systems.



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