RESPONSES OF SOCKEYE SALMON (*Oncorhynchus nerka*) EMBRYOS TO INTRAGRAVEL INCUBATION ENVIRONMENTS IN SELECTED STREAMS WITHIN THE STUART - TAKLA WATERSHED

by

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to the required standard

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ABSTRACT

Before impacts of forest harvesting can be identified, the natural physical and biological influences on incubation processes must be understood within interior British Columbia watersheds. The early Stuart stock of sockeye salmon (*Oncorhynchus nerka*) utilize the most northerly nursery habitat of the Fraser River sockeye stocks. This has led to speculation that production may be limited by high overwinter incubation mortality. An *in situ* incubation study was conducted on four adjacent tributaries of the Stuart - Takla watershed (Kynock, Forfar, Gluskie, Bivouac creeks), during the 1993 and 1994 broodyears.

The study objective was to estimate overwinter survival of sockeye salmon embryos within various redd micro-environments. It was hypothesized that spawning salmon select incubation sites based on environmental cues to optimize egg to fry survival. Egg to pre-emergent fry bioassays, in conjunction with microhabitat environmental monitoring, were implemented to define a range of natural spawning conditions and their relative contribution to fry recruitment.

Results demonstrate that high quality, relatively invariant incubation environment resulted in the lack of classical relations observed in previous studies between incubation parameters and survival. Physical processes (i.e. hydraulic regime, bedload characteristics) and biological processes (i.e. mass cleaning by high densities of spawning adults) result in uniformly high quality

gravel conditions with permeabilities, surface water interchange, and intragravel dissolved oxygen levels associated with high incubation success. Alternative hypotheses of random egg deposition and unlimited high quality habitat were rejected due to; 1) observed spatial preferences and, 2) expansion/contraction of range under different annual population sizes.

Sockeye salmon successfully spawned over a wide range of habitats. High density spawning habitat was the downstream end of pools at the pool riffle interface. Habitats utilized to a lesser degree included; riffles, stream margins, intermittent side channels and portions of the off-channel habitat. Survival rates between these habitat types were not significantly different in contrast to predictions generated from optimality models. This was due to the definition of "marginal" habitat. *In situ* redd simulations showed similar intragravel conditions in both low density (i.e. assumed marginal) and high density (i.e. assumed preferred) areas. Spawning adults avoided truly marginal areas with intragravel dissolved oxygen levels below 3.0 mg/l.

A number of adaptations which would optimize incubation success in northern environments were identified within the early Stuart stock of sockeye salmon. Early Stuart sockeye risk energy depletion and seasonal maximum temperatures during migration and spawning. By spawning early in the season (Jul. - Aug.), early Stuart sockeye enjoy advanced embryological development prior to the onset of low water temperatures. Embryos rapidly accumulate the thermal units necessary to hatch, thereby becoming mobile in time

to avoid freezing and desiccation as water-levels decline and reach seasonal minima. Embryos and alevins of the early Stuart stock can apparently tolerate temperature conditions previously considered lethal. Fry successfully emerge in the spring after accumulating less thermal units than any other Fraser river stock. The trade off against this strategy is the effect of unusually stressful migration conditions on the quality and viability of the gametes. Evidence of this trade off was obtained in 1994, when egg survival rates were very low for spawners that arrived late and had suffered severe thermal stress during migration.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

CHAPTER 1 - INTRODUCTION

General Introduction

Sockeye salmon provide one of the most valuable of Canada's Pacific Coast fisheries. Their use by native peoples is of long standing, and commercial fisheries date to the late 1800s (Hart 1973, Ricker 1987). The current commercial harvest of Fraser River sockeye salmon is valued at $260 million annually (Henderson and Healey 1993). Sockeye incubation streams also drain watersheds containing valuable timber. The close association of salmon streams with timbered watersheds creates potential problems for fishery management. Timber harvesting can have negative affects on salmon incubation environments (Hall and Lantz 1969, Ringler and Hall 1975, Platts et. al. 1989).

There has been a long history of coastal-based fish-forestry interaction research projects (FFIRP) within British Columbia (Poulin 1984, Hartman and Scrivener 1990) and the United States (Sheridan and McNeil 1968, Burns 1970, Moring 1975), and only limited study of interior watersheds (Slaney et. al. 1977, Sterling 1985). Given the amount of interior forestry activity and the lack of knowledge concerning over-wintering incubation processes, there is an urgent requirement for ecological studies to guide land-use practices that are appropriate for the specific physical and biological conditions of interior watersheds. To develop such an understanding the Stuart - Takla FFIRP was initiated in 1990 (Macdonald et. al. 1992).

Before any impacts from forest harvesting can be estimated, natural physical and biological influences on incubation processes must be understood within these interior watersheds. This thesis examines the natural incubation environment before logging, with specific focus on spawner habitat selection, the physical incubation environment, and embryo survival.

This introductory chapter reviews the relevant literature concerning the early Stuart sockeye salmon stock, spawner habitat selection, the physical incubation environment and how these factors influence embryo survival. Chapter two describes the study area and methods. Chapter three presents the results of experiments for the 1993 and 1994 broodyears. Chapter four discusses the over-winter incubation success of early Stuart sockeye salmon and associated physical and biological processes. Finally, a summary of conclusions and management implications are presented in chapter five.

Natural History

Incubation survival is influenced by two main factors; 1) how adults choose incubation sites and, 2) the environment within those sites. The remainder of this chapter reviews these factors.

Pacific salmon are anadromous and semelparous. The early Stuart sockeye salmon migration represents an extreme case. This stock migrates to the northernmost Fraser River watershed ($\approx$1 100 km; altitude 691 m; Idler and Clemens 1959), and is the first to commence spawning within this system, (July 20 - August 20; Killick

1955). Females establish oviposition territories and construct several nests, collectively called a redd (Fleming and Gross 1994). The eggs are covered with gravel and the female guards the nest until her death (Van Den Berge and Gross 1986). The period of egg incubation extends through winter with fry emergence occurring from April to June (Hickey and Smith 1991).

Historically the early Stuart sockeye stock has never been large, and has been unusually variable (Cooper and Henry 1962, Cass 1989). The construction of fishways at Hell's Gate, coupled with regulatory protection in the commercial fishery had increased the average size of the run about seven times by 1961 to 328 000 (average all cycle years). Pre-1948 abundances averaged less than 50 000 (Cooper and Henry 1962). Since 1952, returns have been highly variable with no trend in abundance (Cass 1989). Spawning escapements on the dominant cycle averaged 208 000/yr and ranged from 23 000 in 1965 to 582 000 in 1949 (Cass 1989). The other three cycle years had average escapements between 17 000 and 51 000 (Hickey and Smith 1991). The total early Stuart production capacity in terms of postulated spawning area has been estimated at 632 000 spawners (Anon 1988). With average sockeye escapements of 208 000 there appears to be much under-utilized production capacity (Langer et. al. 1992).

Environmental Factors Affecting Incubation Survival

The early Stuart stock of sockeye salmon utilize the most northerly spawning habitat of the Fraser River salmon stocks. There

3

is also an apparent under-utilized production capacity. This had led to speculation that production of the early Stuart stock of sockeye salmon may be limited by environmental factors. These potential limitations to sockeye production has raised interest in developing an enhancement facility to increase fry production (SEP-Engineering 1988, Langer et. al. 1992).

This thesis examines those factors which may impact incubation survival and fry production. Nest "quality" presumably affects embryo survival. The survival rate to pre-emergent fry reflects the severity of the environmental conditions and the adaptability of the fry (Koski 1975). The environmental factors generally considered to affect egg to emergence survival are water discharge (Hunter 1959, McNeil 1968, 1969), permeability and gravel quality (see Chapman 1988 for review), dissolved oxygen (Alderdice et. al. 1958, Koski 1966, 1975, Bjornn and Reiser 1991), temperature in the incubation environment (Brannon 1987, Velson 1987, Beacham and Murray 1990), stability of the gravel bed (Hunter 1959, McNeil 1966, Lisle and Lewis 1992), and upwelling groundwater (Kogl 1965, Hansen 1975, Leeman 1993).

Temperature is one of the primary physical factors influencing the life history traits of Pacific salmon (Brannon 1987, Burgner 1991). Numerical data (*Oncorhynchus* spp.) have been compiled for the influence of temperature on incubation success (Velson 1987). The majority of this database has been derived from British Columbia salmonid hatcheries and laboratory experiments utilizing coastal broodstock. As a result, data on mortality is scarce for

4

stocks and temperatures less than 5 °C (Velson 1987). In general, sockeye embryos and alevins are not well adapted to survive at high incubation temperatures (Murray and McPhail 1988, Beacham and Murray 1990). The estimated upper temperature of 50% mortality for sockeye salmon embryos was 15.5 °C (Beacham and Murray 1990). Based on this composite database the recommended incubation temperature range of sockeye salmon was 4.4-13.3°C (Bjornn and Reiser 1991).

Population-specific differences in developmental biology have been demonstrated and may reflect adaptation to the thermal conditions experienced during development (Beacham and Murray 1987, 1988, 1989, Murray and McPhail 1988). Interior stocks have faster development rates at colder temperatures than do coastal stocks, and hatch earlier (Brannon 1987, Beacham and Murray 1989). High mortalities are common when temperatures are below 1-3°C. However, interior spawning sockeye stocks have higher embryo survival rates at low incubation temperatures (89% @ 2°C) than do coastal spawning stocks (32% @ 2°C), (Beacham and Murray 1989).

The early Stuart stock of sockeye salmon spawn during annual maximum stream temperatures that approach, and may even exceed, upper critical levels for successful spawning (Scrivener and Anderson 1994). Stream temperatures then decline to mid-winter lows which may remain at 0°C for several months, possibly limiting overwinter incubation success (Scrivener and Anderson 1994).

Many experiments and field studies have related the survival of salmonid embryos to substrate composition and the relative amount of gravel fines (McNeil and Ahnell 1964, Koski 1966, Hall

5

and Lantz 1969, Ringler 1970, Ringler and Hall 1975, Dill and
Northcote 1970, Slaney et. al. 1977, Lotspeich and Everest 1981,
Tappel and Bjornn 1983, Tagart 1984, Everest et. al. 1987, Chapman
1988, Scrivener and Brownlee 1989, Lisle and Lewis 1992, Young et.
al. 1991). Substrate composition affects two critical properties of
spawning gravel; permeability and pore size (Tappel and Bjornn
1983, Brownlee et. al. 1988, Chapman 1988, Platts et. al. 1989).

Permeability (ability of particles to transmit water per unit
of time) is a commonly used measure of the suitability of a redd
for successful incubation of embryos (Wickett 1954, 1958, 1970,
Pollard 1955, Terhune 1958, Coble 1961, Koski 1966, Vaux 1968,
Chapman 1988). The more permeable the gravel redd the greater the
intragravel velocity and the greater the supply of oxygen (Wickett
1970, Chapman 1988, Scrivener and Brownlee 1989). Entombment of
embryos and alevins can occur when fine material lodges in gravel
interstices (Koski 1975, Phillips et. al. 1975, Lisle and Lewis
1992).

The primary source of oxygen for the intragravel environment
is the passage of water into and out of the gravel streambed and is
affected by such factors as gravel permeability, gravel depth,
streambed configuration and stream discharge (Vaux 1962, Sheridan
1962, Kogl 1965, Wickett 1954, Sowden and Power 1985). Numerous
studies have led to the consensus that low dissolved oxygen and
reduced water exchange increase embryo mortality (see Chapman 1988,
Bjornn and Reiser 1991 for reviews). Reduced survival could result
from interference with the interchange of dissolved oxygen due to

sediment accretion (Platts et. al. 1989). Riparian-zone substrates in many interior streams, including these study streams, are characterized by large amounts of lacustrine deposits (Slaney et. al. 1977, Sanborn 1994). Therefore, post-logging increases in the delivery of fine sediments is a principle concern of researchers.

Reported critical ranges of dissolved oxygen derived from artificial streams and laboratories were; 0.72 - 3.70 mg/l (Wickett 1954), 0.72 - 7.19 mg/l (Alderdice et. al. 1958), < 5.0 mg/l (Bjornn and Reiser 1991). It is evident from research on more natural systems that dissolved oxygen below some minimum level becomes a major determinant of survival; 6.0 mg/l (Koski 1966), 3.0 mg/l (McNeil 1969, Koski 1975), 5.0 mg/l (Sowden and Power 1985).

Annual variations in the amount and timing of discharge may cause considerable variation in the availability and suitability of spawning grounds (Hunter 1959, McNeil 1968, 1969). Dewatering and freezing of embryos is generally considered an important cause of mortality in those interior streams with midwinter flow minima (Reiser and Wesche 1979, Neilson and Banford 1983, Bustard 1986, Chapman et. al. 1986, Gibson and Myers 1988, Barlaup et. al. 1994). Sockeye salmon can detect upwelling water patterns (Tautz and Groot 1975, Burgner 1991), and may limit their spawning distribution to areas of warm water upwelling or groundwater seepage to minimize deleterious effects from cold stream water (Kogl 1965).

Incubation Habitat Selection

Although environmental quality ultimately determines if a

fertilized egg will survive to produce a fry, the opportunity to survive is influenced by the behaviour of the parents. It has been found consistently that relatively high proportions of salmon runs spawn in certain areas of streams while other areas have a low percentage of the run (Hunter 1959). The precise homing ability of individuals to natal spawning grounds, and the narrow time window over which spawning may be successful, usually results in large numbers of individuals competing for limited nest sites (Foote 1990).

A widely accepted theory in fisheries management is the "marginal habitat theory", derived from optimality models of habitat selection (i.e. Ideal Free Distribution, Fretwell and Lucas 1970; Density-Dependent Habitat Selection, MacCall 1990; Gradation In Habitat Quality, Hilborn and Walters 1992). This theory predicts that sockeye salmon select spawning microhabitat with the most suitable characteristics, and only move into "less desirable" areas under crowded conditions (Hunter 1959). If areas not used when runs are small have relatively poor conditions for eggs and alevins, then marginal habitat exposes animals to increased risk of mortality (Merrell 1962, McNeil 1968). Marginal areas are those regions which might not consistently provide spawning area either by being exposed (i.e. desiccation and/or freezing) or by being exceptionally poor incubation environment (i.e. low dissolved oxygen, excessive fines)(Hunter 1959).

A number of studies support the predictions derived from marginal habitat theory. First, embryo survival can vary widely

among nests and is often correlated to environmental parameters (Koski 1975, Scrivener 1988, Van Den Berge and gross 1989). Secondly, evidence suggests that competition increases with nest site quality (Foote 1990) and as densities increase, territory area decreases (Tautz 1977, Schroder 1982, Fleming and Gross 1994). While mature females can maximize embryo survival by depositing their eggs in a high quality nest site (Fleming and Gross 1989), the number of spawning sites is often limited promoting territorial behaviour (Foote 1990). This results in an increasing proportion of spawners occurring in less desirable areas as densities increase (Ricker 1954, Hunter 1959, Larkin 1977, Schroder 1982, Neilson and Banford 1983, Chapman et. al. 1986). Average breeding success declines with density, whereas variance in female success increases (Fleming and Gross 1994). This results in an asymptotic number of recruits as spawner numbers increase (Hilborn and Walters 1992). Expansion and contraction of population range or differential utilization of marginal habitat with changes in population abundance is a commonly observed phenomenon associated with such optimality models (Hunter 1959, McCall 1990).

Objectives

The general objectives of this study were to; 1) define natural incubation conditions in a set of interior experimental streams which had experienced minimal anthropogenic impacts and, 2) determine responses of embryos to qualitative and quantitative differences in the various redd micro-environments in which sockeye

9

spawn. This thesis tests the specific hypothesis that spawning salmon select incubation sites based on environmental cues to optimize egg to fry survival in northern environments. Egg to pre-emergent fry bioassays were placed in "preferred" and "marginal" habitats. Habitat classification was determined by observations of qualitative habitat parameters and the spatial distribution of spawners (relative densities), within each experimental reach. Environmental monitoring was implemented to determine the range of natural spawning conditions and the responses of embryos to hypothesized differences in the various redd micro-environments.

Such an approach makes two assumptions. First, individual fish must be able to perceive and respond to detectable gradients of "suitability". Second, spawning salmon measure suitability by using environmental cues such as dissolved oxygen, waterflow, temperature and substrate. These assumptions lead to the general prediction that preferred habitat will have a higher quality and higher egg to pre-emergent fry survival rate, than marginal habitat. Several specific predictions are made: 1) Spawner distribution and egg to emergence survival correlated to the quality of physical parameters being selected for. 2.) Contagious spawner distribution, as a result of physical parameters. 3.) Coarse scale longitudinal gradient of physical parameters and incubation survival within a creek. 4.) Micro-scale gradient of physical parameters and incubation survival across the margins of a creek. 5.) Density-dependence reflected as spawners being forced

10

into marginal sites with poorer quality environmental parameters and lower incubation success.

These predictions are falsifiable under several alternative scenarios. First, it could be that egg deposition is random (spawners not selecting incubation sites based on environmental cues to optimize egg to fry emergence survival). Secondly, redd locations may not be limited. The study streams may have unlimited high quality incubation habitat relative to potential abundance of spawners. Finally, rather than selecting sites to optimize incubation success as hypothesized, spawners may be selecting sites to optimize the spawning act. This alternative hypothesis presumes the habitat requirements for spawning may conflict with the habitat requirements for successful incubation.

CHAPTER 2 - MATERIALS AND METHODS

Study Area

The Stuart River watershed consists of three major river and lake systems which drain south into the Nechako River. It represents the most northern extent of the Fraser River watershed (Fig. 1). Two sockeye salmon runs to the Stuart system are identified from run timing and spawning distribution. The early Stuart stock utilizes more than 30 tributaries, primarily to Takla Lake and Middle River (Lat. 55° 00' N, Long. 125° 50' W.). Four adjacent tributaries (Bivouac, Gluskie, Forfar, Kynock creeks) were chosen for this project (Fig. 2; Bernard et. al. 1994).

Comprehensive watershed descriptions of the study streams are in Harder et. al. (1989), Hickey and Smith (1991), Langer et. al. (1992), and Macdonald et. al. (1992). Briefly, watersheds are in the Hogem Range of the Omineca Mountains, the northern end of the sub-boreal spruce biogeoclimatic zone (BCMFL 1988). Annual precipitation is ≈50 cm and occurs almost exclusively as snow from November to March (Macdonald et. al. 1992). Vegetation cover is predominantly mature spruce/pine forest. Study watersheds are small streams which have no flow stabilizing lacustrine features. Twenty-six of the 33 early Stuart spawning streams fall into this category, representing 44% of the available spawning habitat for the stock (Langer et. al. 1992). Each stream used in this study represents ≈1-7% of the estimated total spawning capacity. Escapements to these three streams represent from 8-42% of the

12

Figure 1. The Fraser River watershed depicting the location of the Stuart - Takla watershed.

13
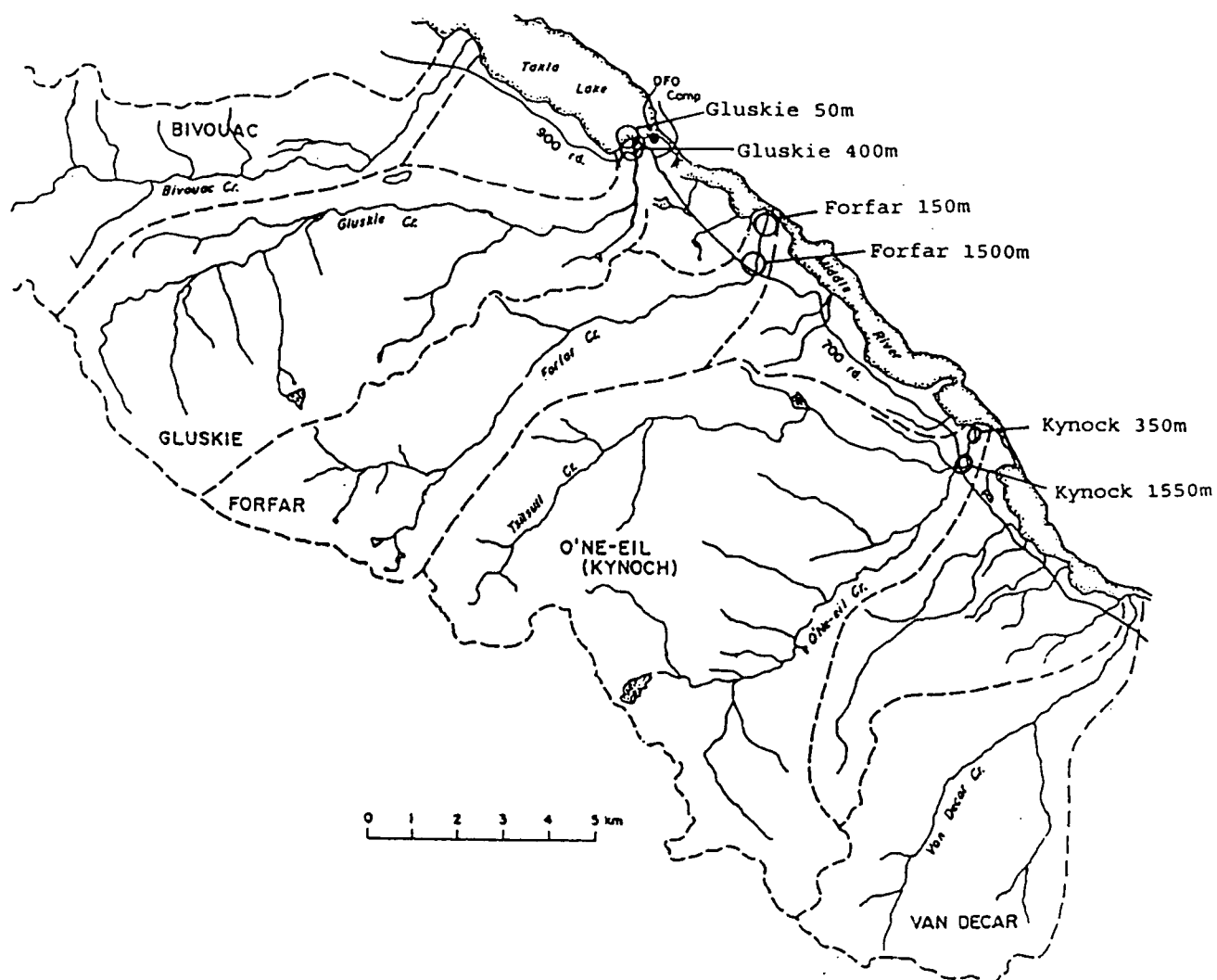
Figure 2. Experimental study area showing Bivouac, Gluskie, Forfar, and Kynock creeks and selected intensive sampling reaches.

14

entire early Stuart escapement (Langer et. al. 1992).

Gluskie Creek has a total watershed area of 55 km^2 and is approximately 19 km long. The lower 0.8 km has a gradient of 1-2%. The upper stream has a gradient of 11% or greater. Estimated usable spawning area is 11 000 m^2 with spawning capacity estimated at 18 000 adults assuming a 50:50 sex ratio and optimum density of 2 spawners/m^2 (Langer et. al. 1992). Gluskie represents 3% of the total estimated production capacity, yet represents between 8-14% of the entire early Stuart escapement. Escapements frequently exceed 10 000 fish (Langer et. al. 1992).

Forfar Creek has a total watershed area of 42 km^2 and is approximately 18 km long. The lower 2 km has a gradient of 1-2%. The upper creek has a 5% or greater gradient. Estimated spawning area is 10 000 m^2, with spawning capacity estimated at 18 300 adults. Forfar Creek represents 3% of the total estimated production capacity, yet represents between 9-18% of the entire early Stuart escapement. Escapements frequently exceed 10 000 fish (Langer et. al. 1992).

Kynock Creek has a total watershed area of 75 km^2 and is approximately 15 km long. The lower 1.6 km has a gradient of 0.5-2%. The upper creek increases to 7-8% by 3 km. Estimated spawning area is 23 000 m^2 with spawner capacity estimated at 47 600 adults. Kynock Creek represents 7% of the total estimated production capacity, yet represents between 9-42% of the entire early Stuart escapement. Escapements frequently exceed 15 000 fish (Langer et. al. 1992).

15

Bivouac Creek has a watershed area of 51 km^2 and is approximately 18 km long. The lower 2 km has a gradient of 1.5%, then increases to 4%. Estimated spawning area is 3 000 m^2 and spawner capacity 5 700 adults. Bivouac Creek represents 1% of the total estimated production capacity, and represents between <1-3% of the entire early Stuart escapement. Escapements are generally < 1 000 fish (Langer et. al. 1992).

Materials and Methods

The main experimental approach was to; 1) map expected habitat suitability (i.e. redd distribution), 2) plant egg capsules to measure space/time variations in survival rate and, 3) monitor environmental parameters to determine their influence on the expected survival patterns.

Egg Capsule Implantation Experiment

i.) Site Selection

Two study reaches were selected in each of Gluskie, Forfar and Kynock creeks, for an initial total of 6 study reaches. Bivouac Creek was added to this study design in 1994. Study reaches were selected to; 1) contain pool-riffle-off/channel habitat, and 2) be representative of the lower floodplain reaches and mid-watershed reaches. Lineal distribution and abundance data for the 1992 broodyear indicated the study reaches were part of the core spawning habitat that occurred from the creek mouth to the 1 230 m, 2 550 m, 2 580 m points within Gluskie, Forfar and Kynock

creeks respectively (Tschaplinski 1994).

The study reaches were partitioned, in relative terms, into low and high utilization spawning habitat. Salmon observed displaying spawning behaviours at regular intervals (Tautz and Groot 1975), had their redds marked by wooden stakes. The capsule implantation sites were then selected based on expected spawner habitat utilization. High utilization habitat was considered "preferred", while low utilization habitat was considered "marginal". Two representative *in situ* redd simulations (2m^2), (one marginal, one preferred) were then constructed within each study reach for an initial total of 12 redd simulations (Appendix A).

ii.) Incubation capsules

Various methods to estimate incubation survival are described in the literature. These include excavation of natural or artificial redds (Slaney et. al. 1977, Gustafson-Marjanen and Moring 1984), redd capping (Koski 1966, Tagart 1984) and trapping of downstream migrants (Fish. Res. Bd. Can. 1956, Anon 1968, Hickey and Smith 1991). Survival estimates derived using these methods may be biased due to several factors; 1) decomposition of unsuccessfully developed eggs before recovery, 2) scavenging, 3) predation, 4) intragravel migration or, 5) over-estimation of egg deposition. Alternatively, eggs may be implanted into the gravel in porous containers (Vibert 1949, Slaney et. al. 1977, Scrivener 1988, Groot 1989, Perkins and Krueger 1994). This "bioassay" technique is appropriately designed to indicate the quality of

17

spawning habitat. However, chambers often cluster eggs in unnaturally high numbers and the capsules can become traps for sediment and encourage the growth of fungus (Harshbarger and Porter 1979, Bams 1985, Greenberg 1992). In this study, egg development capsules were modelled after Scrivener (1988) and Groot (1989). These capsules mimic egg pocket centrum conditions (Chapman 1988). They also provided sufficient water exchange and spatial separation of eggs to remain free of saprophytic fungi and accumulating fines in coastal British Columbia streams (Scrivener 1988). This capsule design requires minimal supervision, would remain unhampered by ice and the extremes of a northern climate, and could be easily recovered.

Incubation capsules were stainless steel cylinders (37 mm inside diameter) with 2.3 mm diameter holes set at 2.0 mm centres. The ends were covered with snug-fitting polyethylene test caps with numerous 2.3 mm holes. A colour coded wire leading from the capsule to the gravel surface marked the capsule site and assisted with retrieval. Two lengths of capsule were utilized; a standard (length = 12 cm) and a longer version for behavioral work (length = 46 cm). Behaviour capsules consisted of two 23 cm sections clamped together vertically (Fig. 3).

iii.) *Fertilization Procedure*

Pooled sockeye salmon gametes (4♀, 4♂) were collected from each creek during spawning. Ova were selected from ripe females (loose eggs easily extruded by gentle abdominal pressure applied
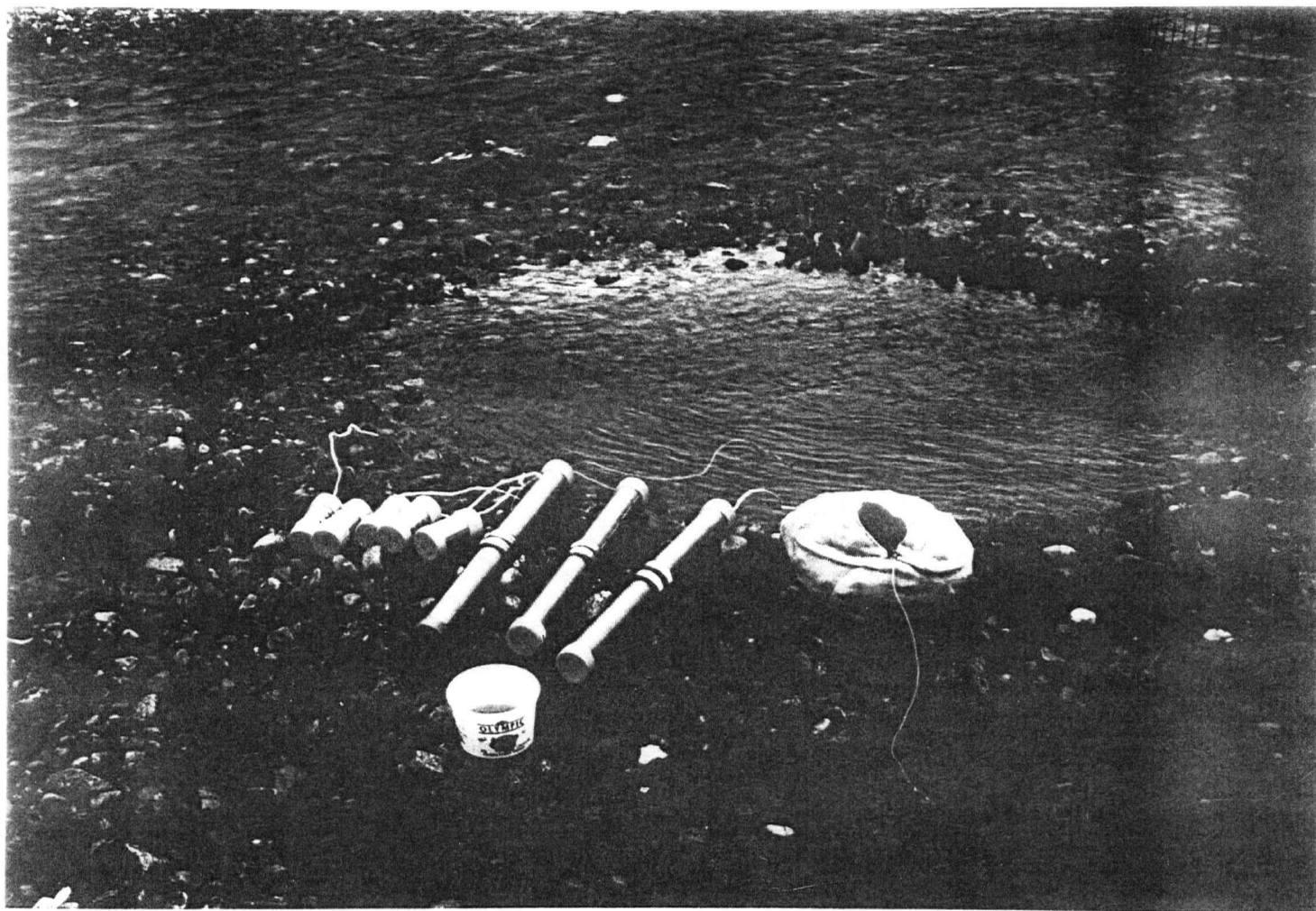
Figure 3. Egg incubation capsules and incubation bags utilized as
bioassays (from left to right; standard capsules - 12 cm
length, Behaviour capsule - 46 cm length, incubation bag -
volume 0.2 m^3). Note redd stranding simulation excavated in
background (area - 2m^2).

anterior to posterior). Fish were carefully examined for maturity and any female that appeared to be partially spawned or immature was not used. Fish of either sex with severe wounds, physical abnormalities, or in generally poor condition were also rejected. Gametes were stored separately in polyethylene containers which were maintained at moderate temperatures (6-11 °C) within gamete transport boxes. Gametes were fertilized using the wet method incorporating an isotonic sodium bicarbonate rinse (Wilcox et. al. 1984).

Thirty eggs, spatially separated by gravel, were placed in the top 10 cm of each capsule. Capsules ($n_{1993}=32$, $n_{1994}=22$) were planted vertically in each simulated redd at a depth of 20 cm, the previously determined average redd depth (Macdonald et. al. 1992). All planting procedures were completed within one hour of fertilization to prevent mortality due to mechanical shock or agitation (Jensen and Alderdice 1983). Fencing material was secured around each redd simulation to ensure the capsules were not disturbed by the remaining spawners.

Typically, each reach within each creek represented a unique fertilization event. Fertilization success was determined for each fertilization event using randomly selected capsules (n=2) retrieved 48 hrs after fertilization. Periodic random collections of developing embryos ($n_{1993}=10$, $n_{1994}=6-7$ capsules/redd simulation) were made: 1) Late September - early October as water temperatures declined rapidly. 2) Late December during low temperature and flow conditions. 3) Mid-April to coincide with the onset of fry

20

emergence. Development rates were examined utilizing the classification system of Vernier (1969).

Analysis of egg to fry survival involved pooling individual capsule survival rates (percent survival normalized by arcsine transformation; Zar 1984) for each redd/date retrieval by stream, stream reach and site (preferred vs marginal). Testing for between habitat differences in survival was by analysis of variance (ANOVA; SAS 1988). Survival rates were tested for differences between marginal and preferred sites nested within stream and stream reach. Post-hoc multiple comparisons of ANOVA results were done using Duncan's multiple range test (SAS 1988).

iv.) *Environmental Monitoring*

Standpipe monitoring stations established within each study reach in each creek, were utilized to characterize stream and intragravel physical variables. Standpipe monitoring stations within each study reach were based on a stratified design that ensured all stream habitat types were sampled (stream margin, thalweg, pool, off-channel). Standpipe monitoring stations were also located within the "marginal" and "preferred" redd simulations where egg capsules were implanted. A total of 10 to 26 standpipes, depending on reach, were sampled for each reach in each sample period (Appendix A). Sampling was undertaken before spawning (July 1-13) and during each embryo collection period (late September, late December, April).

Following a method developed by Terhune (1958), a standpipe

21

was driven into the substrate to a depth of 20 cm to collect intragravel dissolved oxygen, temperature and permeability measurements. An interior sealing rod was used to prevent contamination by surface water during the installation of the pipe. Temperature and dissolved oxygen were measured inside and adjacent to the standpipe using an Oxyguard probe with a water-stirrer. At each standpipe location stream velocity and depth measurements were made as well as visual estimates of the size of surficial streambed material. Relative gravel permeability was determined by pumping water from the standpipe for a known length of time (≈ 5 sec) over a pre-determined head (1").

Physical parameters were examined for differences on a macro-environmental scale (watershed), meso-scale (reaches within watersheds) and, on a micro-habitat scale (habitat type within reaches). Multiple linear regression analysis was used to test the relative significance of environmental variables measured at incubation locations in relation to their corresponding embryo survival. Post-hoc simple linear regression was used to examine the significance of each environmental parameter independently.

Additional Incubation Experiments

i.) *Stream Fidelity Experiment*

A fully crossed gamete incubation program was instituted within the general habitat study of 1993. The objective was to test if genetic differentiation between broodstock from the study creeks may impair ability of eggs to survive in nearby creeks. Within each

creek redd simulations (upper reach, preferred habitat) were utilized (Appendix A). In addition to the 32 capsules of a creek broodstock, 10 additional capsules were planted with eggs from the other two study creeks. These 30 capsules (n=10 from each of the creeks) were left for the incubation duration and retrieved during the final sampling period (April 1994). A comparison of gamete viability between broodstocks, across three study streams was estimated under identical rearing conditions (1 way ANOVA; SAS 1988).

ii.) *Incubation Transects*

In 1994, bank to bank transects of incubation capsules were installed within the Kynock 1550 m study reach (Appendix A1). Site selection (n=11 *in situ* redd simulations) was based on qualitative and quantitative differences in habitat parameters, regardless of expected spawner utilization. The objective was to expand the range of environmental parameters beyond those selected by spawning adults. Based on the 1993 results it was hypothesized that a "threshold" level existed beyond which spawning females would not utilize the habitat. It was further hypothesized that lower survival rates would result from the lower quality habitat beyond these thresholds. Either 6 or 8 capsules were installed at each of the 11 redd simulations. Capsule retrieval (n=2-3 capsules) followed the standard sampling protocol. Environmental parameters were measured as previously described, within each simulated redd.

iii) *Capsule effects*

Alternative perforated containers were designed to assess the effect of the incubation capsules on egg to fry survival (Fig. 3). These incubation "bags" were adapted from Perkins and Krueger (1994). Mesh bags were much larger ($\approx$.2m^3) and were constructed from mark-rosette cloth. Substrate was not selected for optimum qualities but to represent the *in situ* composition. This alternate redd simulation tested the concern that selection of only good quality substrate to put into incubation capsules created micro-habitat conditions that unnaturally influenced survival. Two "bags" were paired with 8 standard capsules in 5 locations arrayed across creeks (Appendix A). Capsule effects were then examined by paired t-test (Zar 1984).

iv.) *Intragravel Behaviour of Alevins*

Constriction of larval movement within incubation capsules could decrease incubation success if subgravel behaviour of alevins (i.e. vertical/lateral migration) occurs in response to changing environmental conditions. Five redd stranding simulations containing 6 behavioral incubation capsules and six standard incubation capsules were arrayed across creeks in 1994 (Appendix A). The design of the behavioral incubation capsules would permit the vertical movement of larvae (i.e. 46 cm of vertical distance versus 12 cm in standard incubation capsules). Locations were chosen based on observations during the 1993 studies that would likely be impacted by dewatering or freezing. Stranding

simulations were generally located within stream margins or shallow gravel bars containing low density spawning activity and post-spawning exposed surficial substrate.

Collections of developing embryos were made; 1) prior to hatching in late September as waterlevels and temperatures began to decline rapidly and, 2) during the alevin stage in February during minimum flow and temperature conditions.

Within each simulated redd, during both retrieval periods, environmental parameters were measured as previously described. The effects of dewatering and freezing on larval behaviour and survival rates was inferred from; 1) determination of the pre-hatch vertical distribution and survival of embryos, 2) contrasting the vertical distributions of embryos and alevins within behaviour capsules in relation to key environmental parameters (i.e. waterlevel, temperature) and, 3) examination of survival rates in relation to environmental conditions.

CHAPTER 3 - RESULTS

Spawner Abundance and Distribution

The early Stuart escapement typically occurs between July 22 to August 15, and peak spawning activity occurs between August 3-13 (Fig 4; G. Smith, D.F.O., Stock Assessment Group, unpubl. data). Escapement estimates for the study creeks were very different between the two years of study (Table 1; T. Whitehouse, D.F.O., Stock Assessment Group, unpubl. data). Based on estimates for usable spawning area optimum escapement levels were exceeded in 1993 (density = 3.46 spawners/m^2), while 1994 was well below this level (density = 0.30 spawners/m^2). During the high density broodyear, abundances were dramatically higher at all locations, and distributions were extended a further 1.2 - 2.0 km upstream to where obstructions blocked further movement (P. Tschaplinski, M.O.F., Research Branch., per. comm.).

Redd distributions within all study reaches demonstrated spatial preferences (n=6). High density spawning habitat ("preferred") was consistently at the tail of pools in the pool-riffle transition. Low density spawning habitats ("marginal") included; riffles, stream margins, intermittent side-channels and portions of off-channel habitat. These spatial preferences were consistent over both study years (Fig. 5, Appendix A).
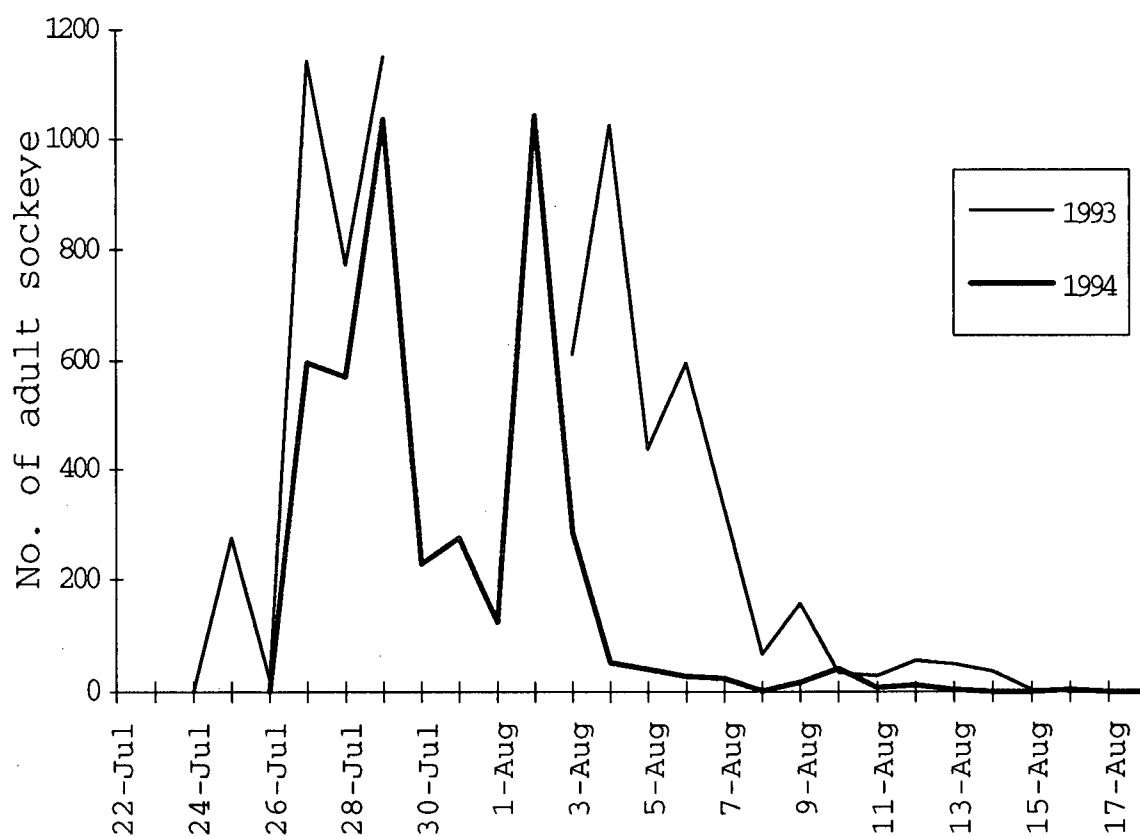
Figure 4. Adult sockeye arrival timing at Forfar Creek mouth.
Number of adult sockeye was the daily total sockeye through
the fence at the mouth of Forfar Creek. The period July 29 -
August 2, 1993 was unavailable due to a freshet event
removing the counting fence during this period. Daily
escapement was conservatively estimated at 3 000 based on peak
live counts plus cummulative dead (G. Smith, D.F.O., Stock
Assessment Group, unpubl. data).

27

Table 1. Sockeye salmon adult escapement estimates and fry production estimates (T.Whitehouse, D.F.O., Stock Assessment Group, unpubl. data) and corresponding egg to pre-emergent fry survival rate estimates for the early Stuart study streams of Middle River and Takla Lake (1993 and 1994 broodyears).

Creek	1993 Broodyear					1994 Broodyear				
	Bivouac	Gluskie	Forfar	Kynock	Total	Bivouac	Gluskie	Forfar	Kynock	Total
Eff. Females +	23 000	16 749	20 665	20 665	81 265	341	1 950	2 511	2 148	6 950
Escapement ++	46 000	33 498	41 330	41 702	162 530	682	3 900	5 022	4 296	13 900
Density +++	15.3	3.0	4.1	1.8	3.5	0.2	0.4	0.5	0.2	0.3
Fry (x1000) +	-	7 296	12 083	22 737	42 116	-	749	2 700	3 408	6 857
Egg-Fry (%) +	-	13.5	19.1	35.4	22.7	-	11.6	28.9	48.0	29.5
Egg-Pre-emergent Fry Survival (%) *	-	50.9	49.5	45.8	49.0	7.3	27.7	15.6	60.1	28.0

+   D.F.O. Stock Assessment Group, Enumeration Program Estimate, T.Whitehouse unpubl. data

++   Assumes 50:50 sex ratio

+++ Based on Fraser River Sockeye Task Force usable spawning area estimates (Langer et. al. 1992)

*   Based on mean incubation capsule bioassay results
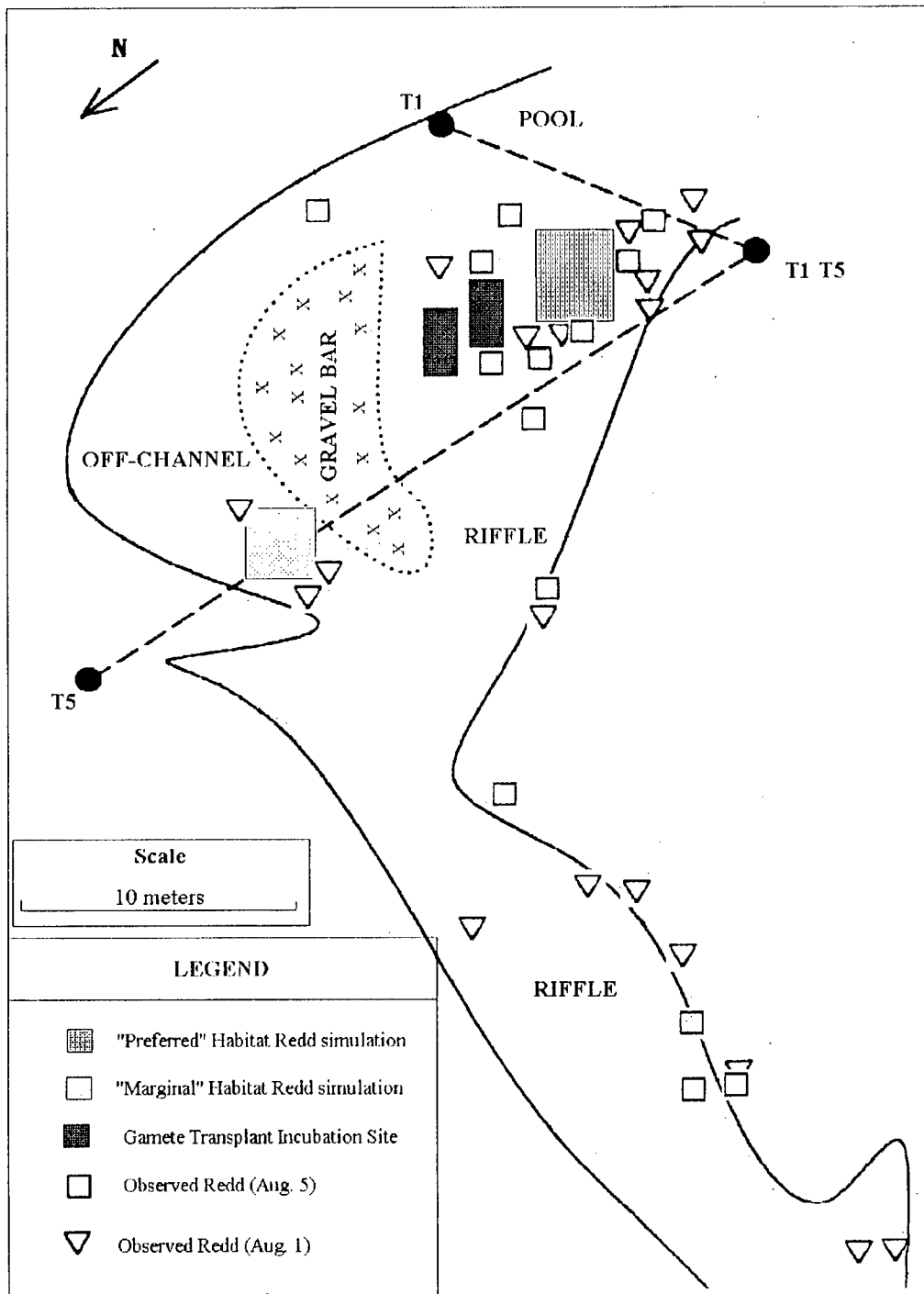
Figure 5. Redd locations determined through ethological
observation (July 31, Aug. 1 and Aug 5 1993) within Gluskie
400 m study reach. Transects 1 and 5, and incubation capsule
locations (redd simulations) were included for reference
points (see Appendix A). Stream wetted surface area was
surveyed Sept. 18, 1993. Note stranded redd locations along
stream margins.

Egg to Pre-emergent Fry Survival

Examination of the sources of variation for embryo survival rates indicated an interaction between broodyear and creek ($p < 0.01$; Appendix B). This means that the data cannot be analyzed across years for each creek in testing for habitat effects. Survival rates were blocked by broodyear, and survival differences between habitats were tested.

The 1993 mean survival rate from fertilization to pre-emergent fry was 49%. Mean survival was 51%, 50% and 46% for Gluskie, Forfar and Kynock creeks respectively. There was no difference between survival rates ($p > 0.05$), and no significant effect of creek ($p > 0.05$), reach ($p > 0.05$) or habitat type ($p > 0.05$).

The mean 1994 survival rate to pre-emergent fry was 27%. There was significant variation in survival rates between creeks ($p < 0.01$), but not reaches within each creek ($p > 0.05$), or habitat type within reaches ($p > 0.05$). Mean survival rate was lowest in Bivouac Creek (6%; $p < 0.05$). Mean survival rates of Forfar (16%) and Gluskie (28%) creeks were intermediate ($p < 0.05$), and all 3 creeks had lower mean survival rates than Kynock Creek (60%; $p < 0.05$; Appendix B).

There were significant differences in mortality rate between the developmental stages ($p < 0.01$). Eighty percent of the mortality occurred in the first 50 days, before hatching (Fig. 6). The 1994 pre-hatch mortality (62.5%) was higher than 1993 (48.1%; $p < 0.05$). The remaining mortality was expressed as unfertilized
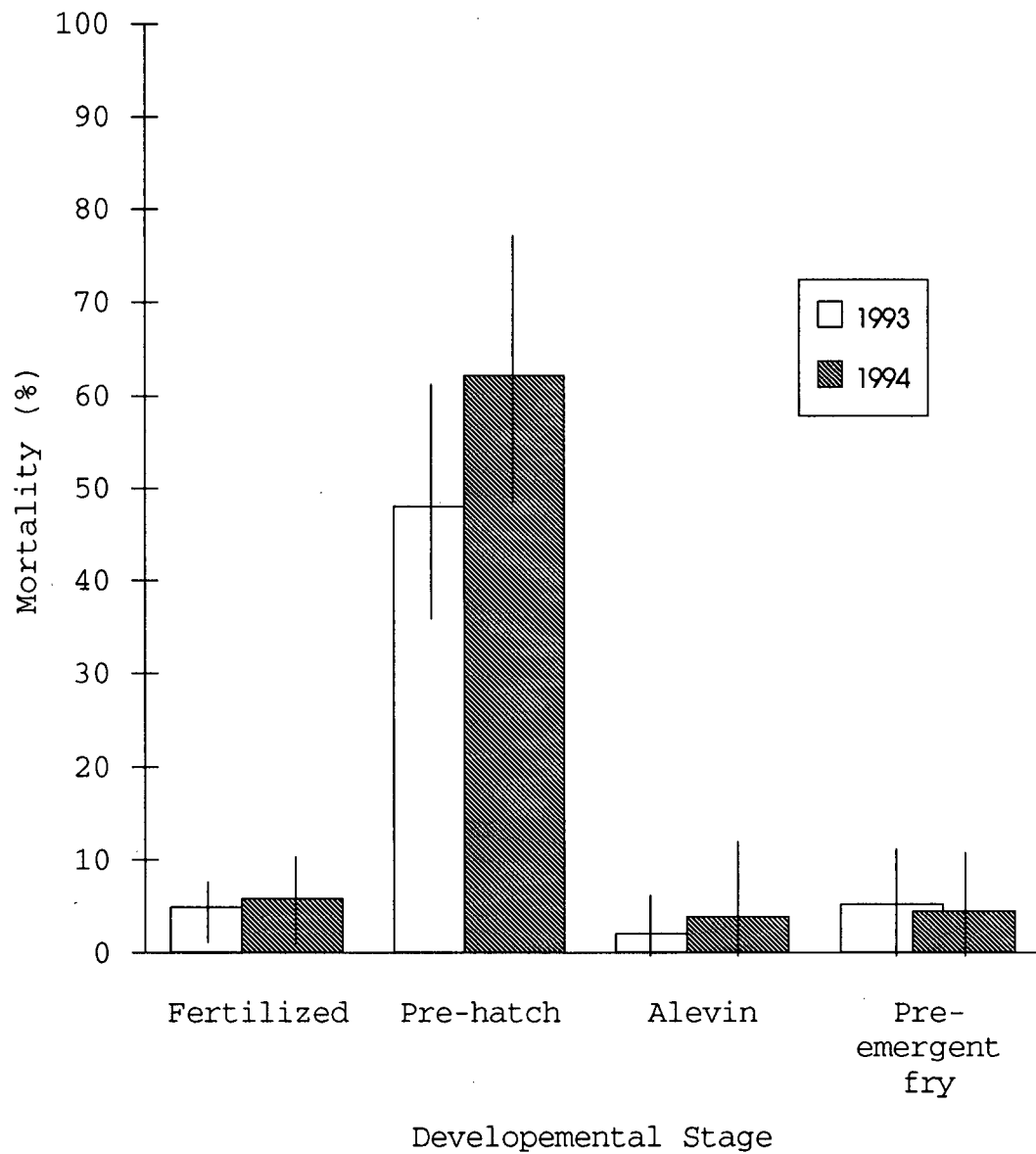
Figure 6. Percent mortality of embryos assessed at the end of each retrieval period for all study streams combined (mean +/- 2*S.E.). Note fertilization = 0-2 days (Aug.), Pre-hatch = 2-50 days (late Sept.), alevin = 50-180 days (late Dec. - Feb.), pre-emergent fry = 180-260 days (mid April).

eggs (8%) and over-wintering processes (12%). The majority of over-wintering mortality occurred when individual capsules were frozen as intragravel waterlevels dropped below the capsule depth (i.e. a simulation of redd stranding). This occurred in mid-winter when water levels were lowest.

Survival rates did not differ between the redd simulation bags (n=10) and associated egg capsules (fig. 7; $p > 0.05$). The redd simulation bags appeared to show less variable survival among study sites than indicated by the capsule data. Fertilization success, determined 48 hours post-fertilization, did not vary between years ($p > 0.05$; Fig. 6). Results of the stream fidelity experiment were non-significant, indicating that any genetic differentiation between creeks does not impair ability of eggs to survive in nearby creeks.

Physical Environment

All incubation environments were relatively invariant, with high quality incubation habitat available at all scales examined. Figure 8 illustrates the visual characteristics associated with representative marginal and preferred incubation habitats. There were no significant differences between these habitats (all reaches, creeks and years combined) in either stream or intragravel parameters (Table 2). While both incubation habitats contain high quality conditions, there was a trend towards lower values within the marginal habitats (i.e. shallower, lower velocity, finer substrate, lower permeability, and lower dissolved oxygen).
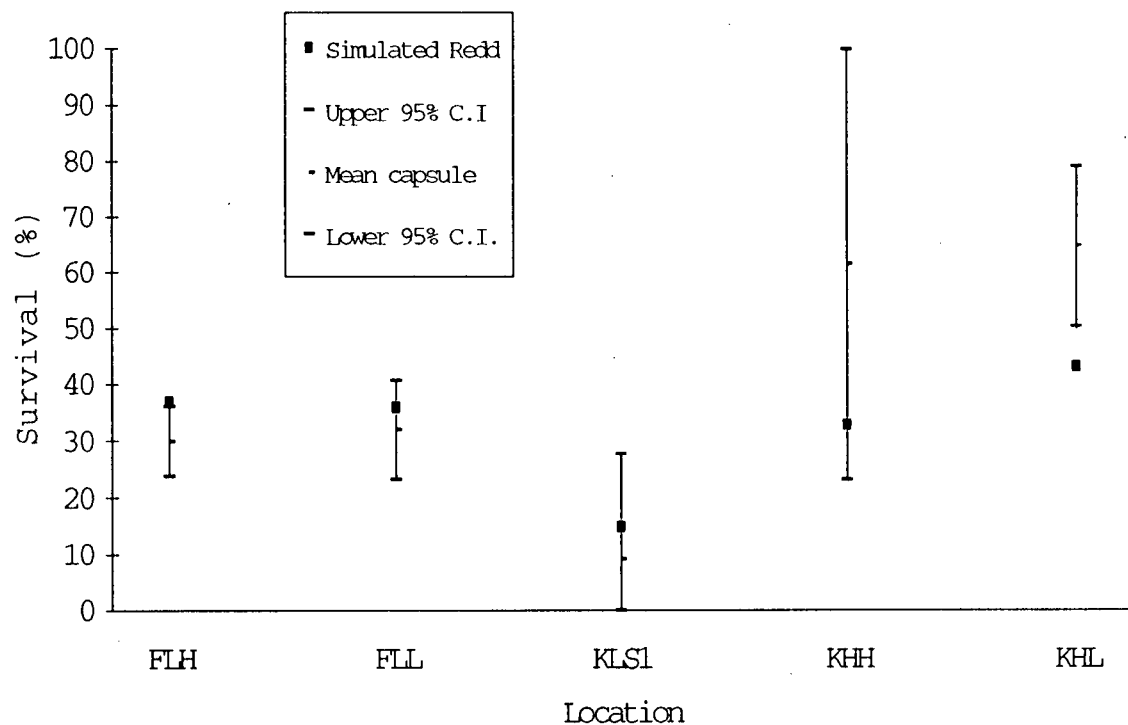
Figure 7. Comparison of survival rate (fertilization to pre-hatch embryos; 50 days) between redd simulation bags (n=10) utilizing representative *in situ* substrate composition and standard egg incubation capsules (mean +\- 95% confidence interval). Incubation locations were arrayed across study creeks (FLH = Forfar 150m preferred redd simulation. FLL = Forfar 150m marginal. KLS1 = Kynock 350m stranding simulation. KHH = Kynock 1550m preferred. KHL = Kynock 1550m marginal.).

33

B.

A.
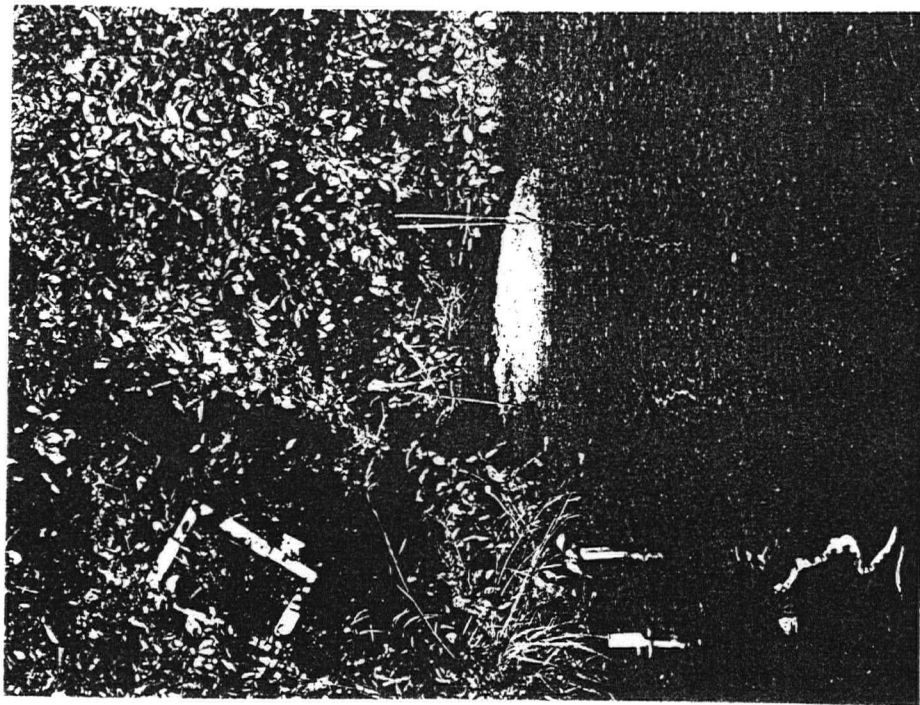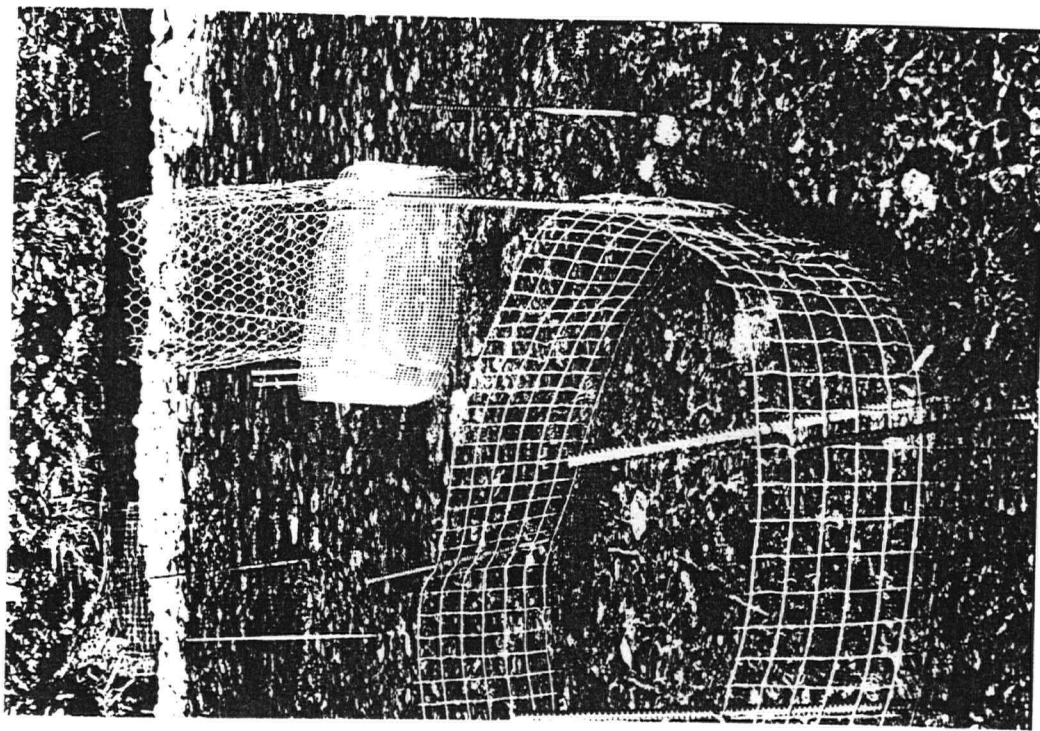
Figure 8. Forfar Creek lower watershed (150 m) redd simulations. Photographs depict conditions typical of a) marginal and b) preferred incubation habitats (photographs were taken 14 days post fertilization).

34

Table 2. Summary of stream and intragravel physical parameters for preferred and marginal redd simulations (all locations, creeks and years combined; n=25).

| VARIABLE | CAPSULE INCUBATION SITE | | p < 0.05 |
	PREFERRED	MARGINAL	
VELOCITY (m/s)	0.19	0.13	
Std. Err.	0.02	0.04	no
Range	0.00 - 0.45	0.0 - 0.71	
n	22	21	
DEPTH (cm)	29.1	20.7	
Std. Err.	4	3.7	no
Range	2.0 -74.0	1.0-57.0	
n	24	23	
STREAM TEMP (C)	3.58	3.4	
Std. Err.	0.65	0.63	no
Range	- 0.1-9.4	-0.1-8.8	
n	25	24	
SURFACE SUBSTRATE	3.41	3.06	
Std. Err.	0.22	0.3	no
Range	1.0 - 4.4	1.0-5.0	
n	18	18	
STREAM DISSOLVED OXYGEN (mg/l)	11.68	11.17	
Std. Err.	0.17	0.29	no
Range	10.3-13.1	7.3-12.9	
n	25	23	
INTRAGRAVEL DISSOLVED OXYGEN (mg/l)	10.76	9.99	
Std. Err.	0.22	0.4	no
Range	8.2-12.4	4.9-12.0	
n	25	24	
PERMEABILITY (ml/s)	21.7	19.3	
Std. Err.	2.8	3.7	no
Range	8.4-50.0	0.0-48.6	
n	16	16	
INTRAGRAVEL TEMPERATURE (C)	3.6	3.42	
Std. Err.	0.65	0.62	no
Range	- 0.1-9.4	0.0-8.5	
n	25	24	

35

The Forfar Creek thermal regime is representative of the annual pattern for natal streams used by the early Stuart sockeye stock (Fig 9; B. Anderson, D.F.O., P.B.S., unpubl. data). Daily stream temperatures rise from 4 - 10°C during June, vary from 8 - 16°C during summer, and drop rapidly in October and remain at 0.0 - 0.5°C throughout winter. Kynock Creek mean spawning period temperatures (July 20 - Aug 20), ($11.7_{1993}/13.4_{1994}$°C) were $\approx$1.0°C higher than either Gluskie (10.2/12.4°C) or Forfar (10.5/12.4°C) creeks (Fig. 10). The 1994 mean spawning temperatures were significantly higher than 1993 ($p < 0.05$). There were no significant differences in stream temperature between either; 1) reaches within a creek or, 2) habitat type.

For all reaches, creeks and years combined, there were no significant differences in intragravel water temperature between incubation locations (Table 2), or habitat types in general (Table 3). During the mid-winter (1993) sample period, the intragravel thermal regime closely parallelled ($Mean_{diff.} = 0.1$°C) the stream thermal regime. No habitat specific groundwater upwelling was detectable from temperature comparisons.

Peak stream flows were generated by snow melt during the spring and by rain storms during the spring and autumn. Low flows were observed from November to March and from mid-July to mid-September (Fig 11; Scrivener and Anderson 1994).

Winter discharges may be as little as 20% of the fall. As seen from the stream wetted surface area approximately 50 days after spawning, redds located in stream margin habitats were susceptible

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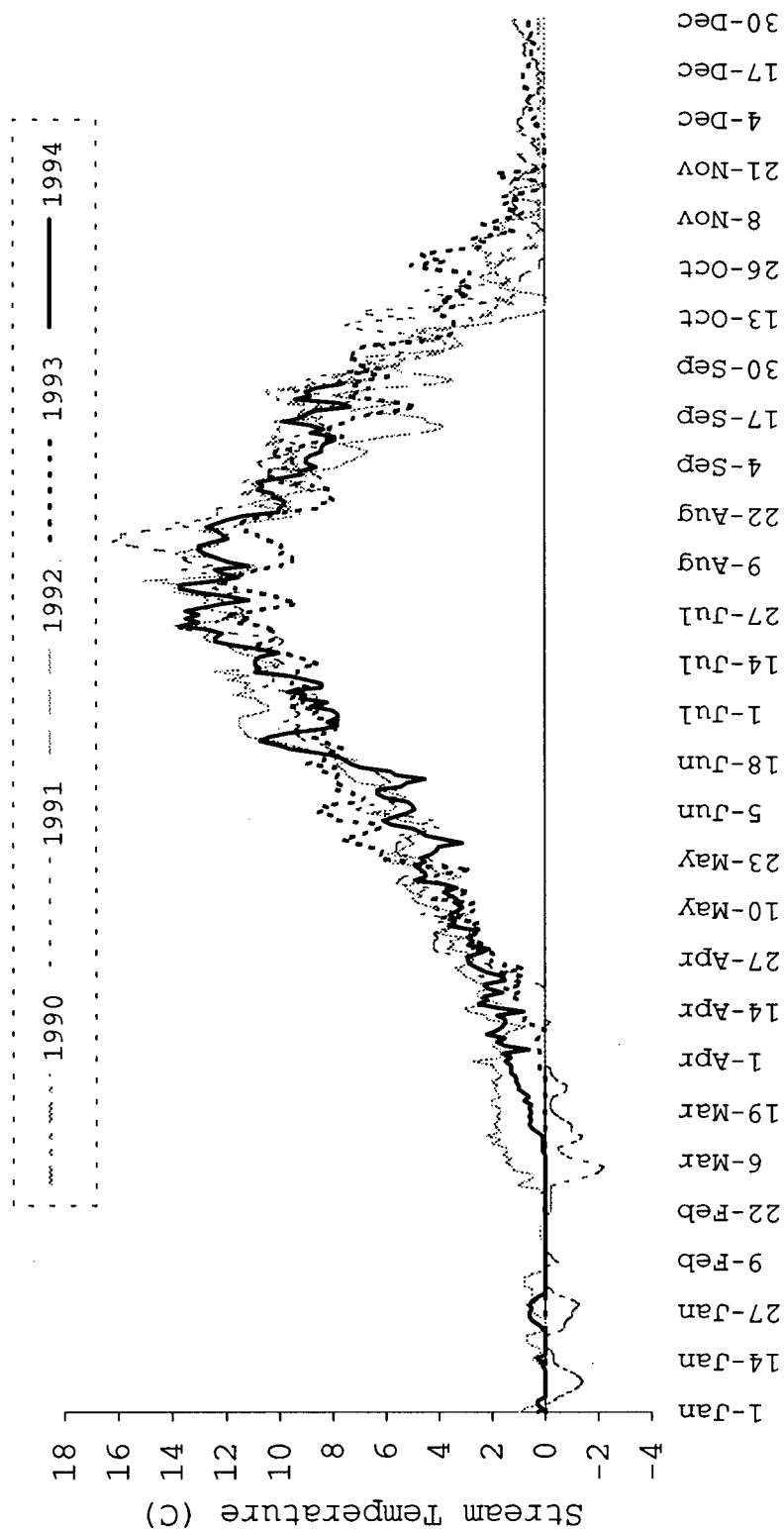
Figure 9. Daily maximum temperatures in Forfar Creek for the period 1990 - 1994 (B. Anderson, D.F.O., P.B.S., unpubl. data).

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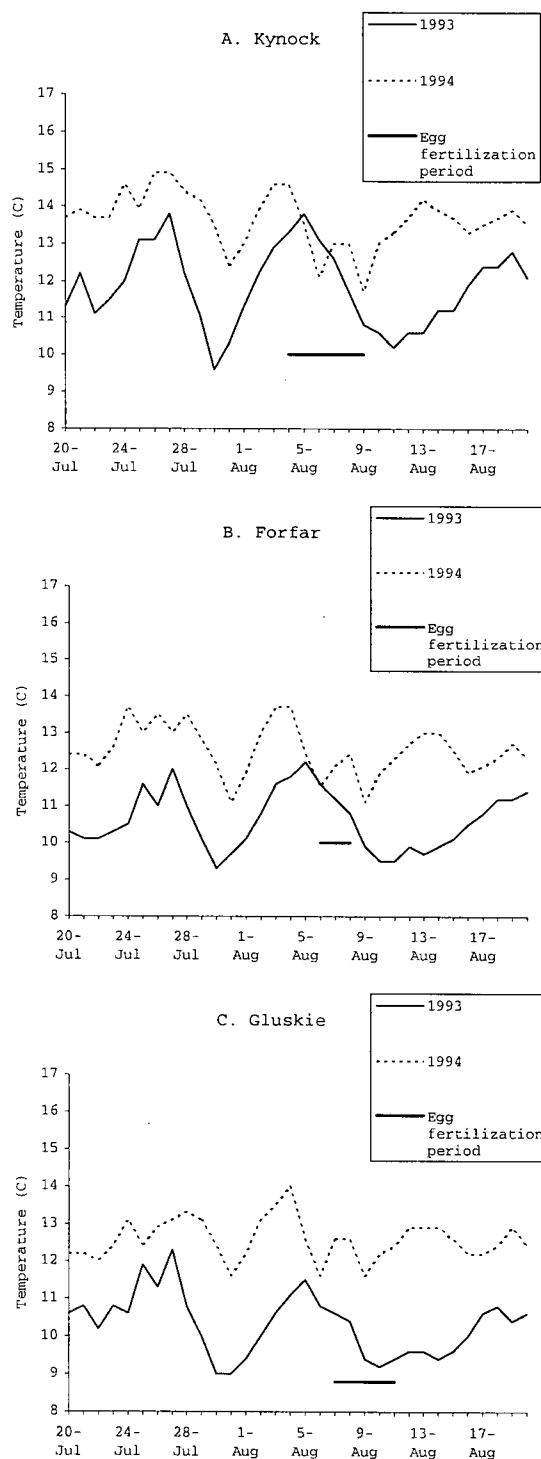
Figure 10. Early Stuart spawning period (20 July - 20 August) daily maximum stream temperatures in; a) Kynock, b) Forfar, and c) Gluskie creeks for the broodyears 1993 and 1994 (B. Anderson, D.F.O., P.B.S., unpubl. data).

38

Table 3. Summary of stream and intragravel physical parameters by general habitat type (margin, thalweg, pool, off-channel) for all seasons (1993-1994), creeks (n=4) and locations combined (n=563).

VARIABLE	MARGIN	THALWAG	POOL	OFF-CHANNEL	P < 0.05
VELOCITY (m/s)	0.29	0.43	0.14	0.08	***
Std. Err.	0.02	0.02	0.01	0.01	
Range	0.01-1.06	0.00-1.45	0.00-0.58	0.00-0.59	
n	166	187	90	100	
Duncan	B	A	C	D	
DEPTH (cm)	18.9	27.5	41.8	25.3	***
Std. Err.	1	1.1	1.9	2	
Range	3.0-64.0	2.0-100.0	2.0-84.0	1.0-132.0	
n	168	190	92	98	
Duncan	C	B	A	B	
STREAM TEMPERATURE (C)	6.7	6.6	5.9	5.8	
Std. Err.	0.3	0.3	0.4	0.4	
Range	-0.1-12.7	-0.1-12.7	-0.1-12.7	-0.2-12.9	
n	171	194	93	98	
INTRAGRAVEL TEMPERATURE (C)	6.7	6.6	6	5.7	
Std. Err.	0.2	0.3	0.4	0.4	
Range	-0.1-12.8	0-12.8	-0.1-12.7	-0.1-12.8	
n	172	193	93	98	
SURFACE SUBSTRATE	3.57	3.99	3.38	2.84	
Std. Err.	0.07	0.05	0.16	0.11	
Range	1.7-5.1	2.0-5.0	1.0-5.2	1.0-5.0	***
n	164	184	73	82	
Duncan	B	A	B	C	
STREAM DISOLVED OXYGEN (mg/l)	10.9	11	11.1	10.4	
Std. Err.	0.1	0.1	0.1	0.2	
Range	9.4-13.3	9.4-13.2	9.1-12.8	3.6-13.0	***
n	171	194	93	98	
Duncan	A	A	A	B	
INTRAGRAVEL DISOLVED OXYGEN (mg/l)	9.5	9.8	9.9	6.6	
Std. Err.	0.17	0.15	0.2	0.38	
Range	0.3-12.8	0.3-12.9	0.3-12.4	0.2-12.0	***
n	172	193	93	98	
Duncan	A	A	A	B	
PERMEABILITY (ml/s)	25.4	25.9	24.9	19.9	
Std. Err.	1.5	1.5	2.5	1.8	
Range	3-125	4-129	6-120	0-82	
n	160	181	60	78	
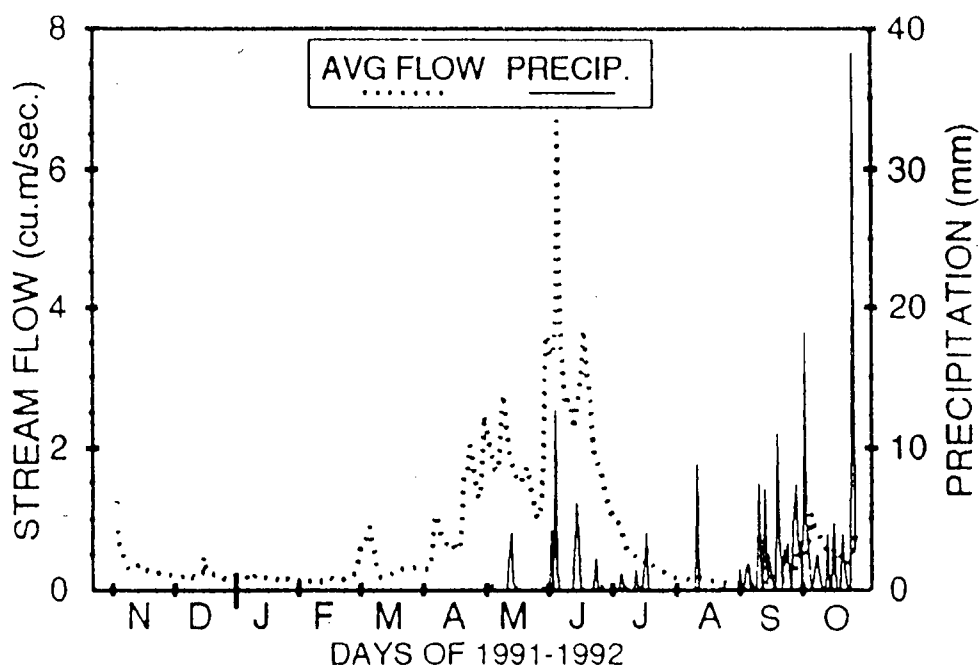
Figure 11. Hydro-meteorological data recorded in Gluskie Creek watershed including mean daily flows for the water-year November 1, 1991 to October 31, 1992 and total daily rainfall for April 27 to October 20, 1992.

to dewatering (Fig. 5). Reach velocities at this point (late September) averaged 30% of those during the spawning period, and redd water depths were similarly reduced.

Results of the environmental monitoring program are summarized by habitat type and sample date in Appendix C1. There were no differences in mean (all sample periods and habitat types combined) velocity, depth, stream temperature, permeability, or intragravel water temperature between study creeks ($p > 0.05$; Appendix C2). There were differences in surface substrate index, stream dissolved oxygen and intragravel dissolved oxygen. All mean values indicated high quality incubation habitat(Appendix C2). The 1994 broodyear was significantly shallower ($p < 0.05$). This was attributed to water impoundment as a result of beaver activity in lower watershed reaches in 1993 (i.e. pool depth; Appendix C1).

Generally, surface substrate composition indices were > 3.4, corresponding to high quality spawning gravel with mean particle sizes of (2 mm - 64 mm). Only off-channel habitat (substrate composition index = 2.8) had a significant proportion of silt and sands (Appendix C1). The range (1.0-5.0) indicates portions of this habitat contained high quality gravel for incubating eggs (Table 3). There were differences in surface substrate composition between reaches ($p < 0.05$). Upper locations were coarser due to increasing gradients and water velocities. Broodyear differences were attributed to water impoundment by beavers during the winter of 1993/1994 in 2 of the 6 study reaches. This resulted in surface deposition of fine sediments.

41

All habitats (table 3) and capsule incubation locations (Table 2) contain mean permeabilities of > 19 ml/s (6,840 cm/hr). Ninety percent of all samples (n = 784) of stream and intragravel dissolved oxygen were > 6.0 mg/l (Fig. 12). There were intragravel dissolved oxygen differences between the two study years (July and Sept. sampling periods $p < 0.05$; $mean_{1993}=9.59\pm0.14$ mg/l, $mean_{1994}=8.49\pm 0.19$ mg/l). This difference was attributed to the higher water temperatures of 1994.

Intragravel dissolved oxygen levels between preferred and marginal incubation habitat were similar ($p > 0.05$; Table 2). Only off-channel habitat had lower intragravel dissolved oxygen ($p < 0.05$; 6.4 mg/l; Table 3). The variance within a study reach demonstrates all habitats contain areas of high quality incubation habitat (Fig. 13).

Effects of Environmental Factors on Incubation Survival

Multiple regression analysis of embryo survival rates on physical variables measured at incubation location standpipes (stream temperature, dissolved oxygen, velocity, depth, surficial substrate index and, intragravel temperature, dissolved oxygen, permeability) failed to detect any significant correlation predictions ($p > 0.05$, $r^2 = 0.17$, n=53). This was a result of; 1) survival between preferred and marginal habitats were not significantly different and, 2) preferred and marginal habitats contained high quality incubation habitat with non-significant differences in environmental conditions. Results of similar

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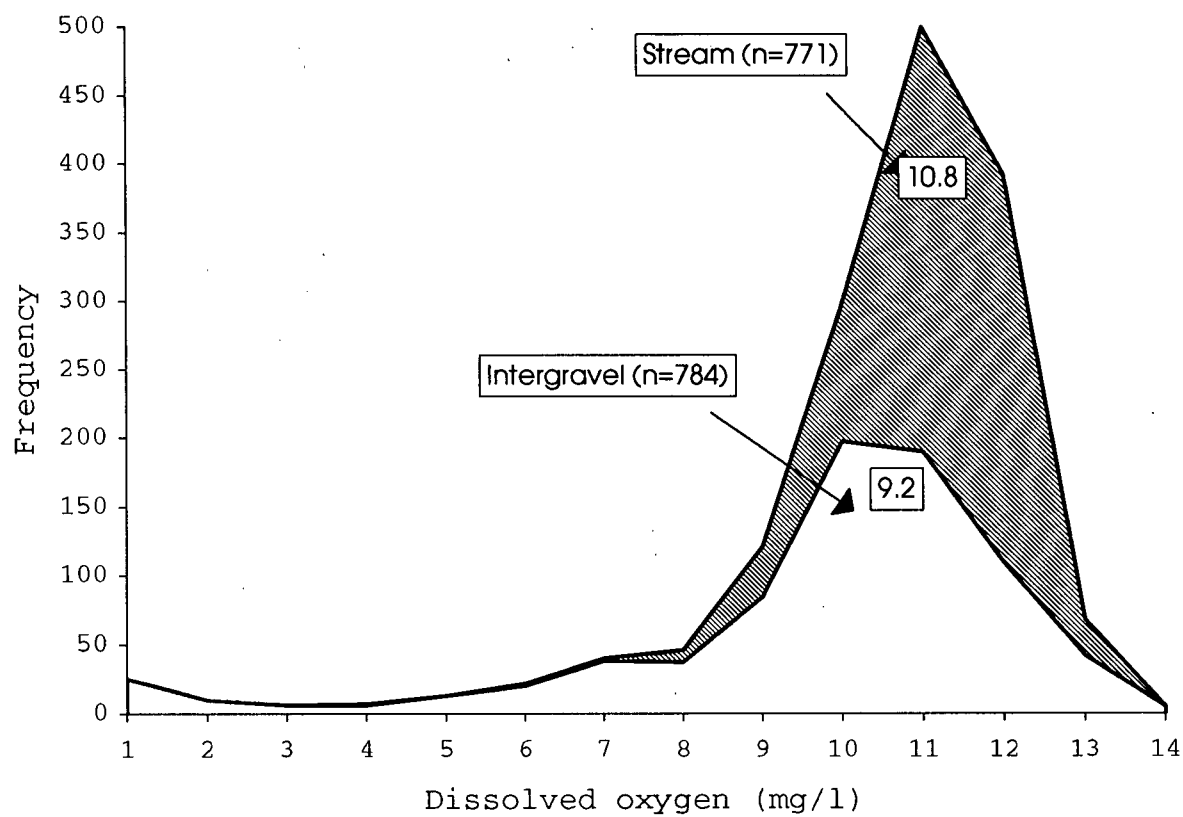
Figure 12. Frequency distribution of stream (n=771) and intragravel
      (n=784) dissolved oxygen measurements within the four study
      streams from the period 1992 - 1995.

43
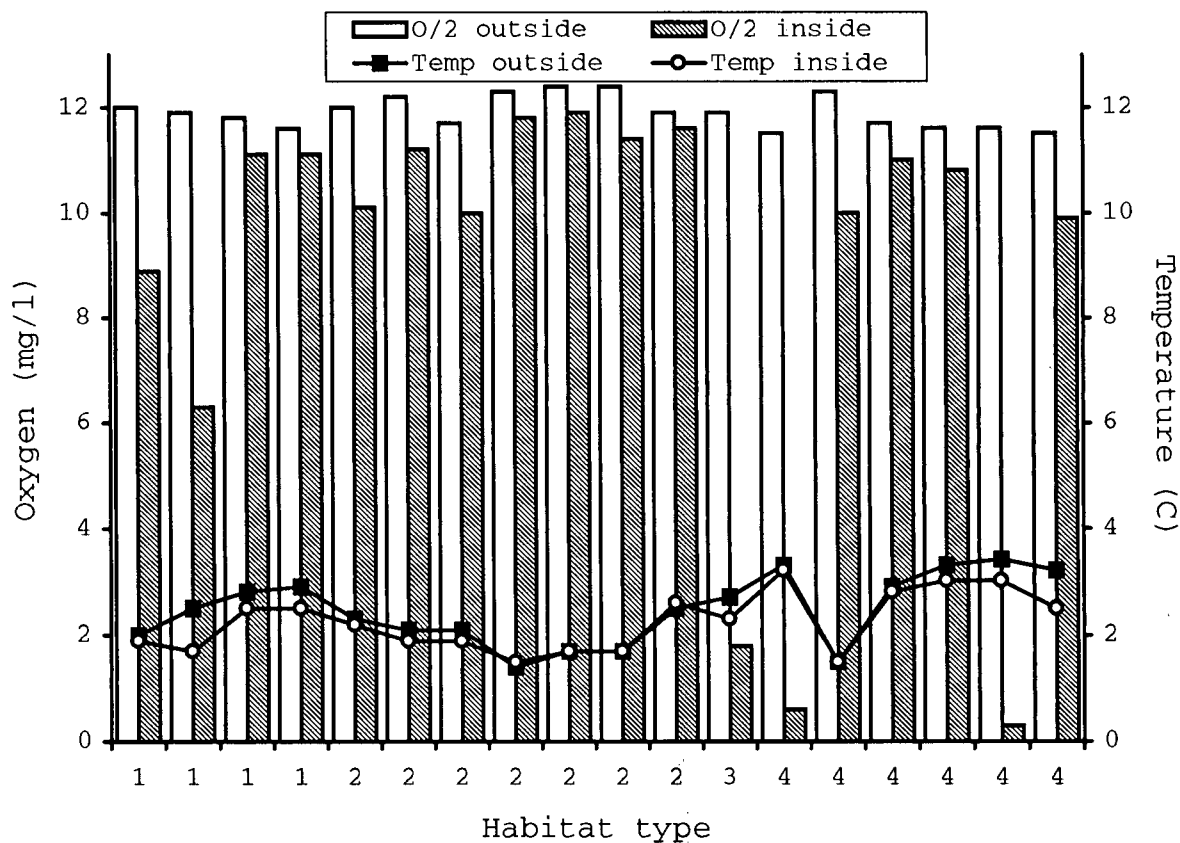
Figure 13. Within study reach variation for dissolved oxygen and temperature for the standpipe sampling grid of Kynock Creek 1550 m (mid-watershed), 4 April 1994. Temperature and dissolved oxygen were measured at an intragravel depth of 20 cm. Standpipes were grouped by habitat classification code (1=thalweg, riffle, 2=margin, 3=pool, glide, 4=off-channel).

survival from low density ("marginal") sites, and high density ("preferred") sites, with obvious visual substrate differences (Fig. 8), yet similar intragravel conditions (Table 2), suggest the visual differences were misleading in terms of actual incubation site quality.

Incubation locations for the 1994 transect study were selected regardless of expected spawner habitat utilization. As a result, the range of environmental parameters associated with incubation locations was expanded. Inclusion of this data within 1994 survival rates resulted in a non-significant multiple correlation prediction (p = 0.06, r^2 = 0.34, n=43). There was a non-significant relationship between intragravel dissolved oxygen and survival rate (Fig. 14). Transect data suggest intragravel dissolved oxygen does not effect survival rate until levels drop below 4.0 mg/l (Fig. 15). Spawning sockeye did not utilize habitat with less than 3.0 mg/l intragravel dissolved oxygen. Embryos placed in these locations did not survive and this relationship is probably not well described by linear regression models.

Multiple regression analysis also indicated a relationship between temperature and embryo survival rate. In 1994, Kynock Creek had significantly higher survival rates (Appendix B) and stream temperatures (Fig. 10). Therefore, at a given sampling time in 1994, the higher survival rates of Kynock Creek were associated with warmer temperatures. This relationship was a spurious result. Regression analysis indicated the difference in mortality patterns for 1993 and 1994 was related to the date fertilized in 1994
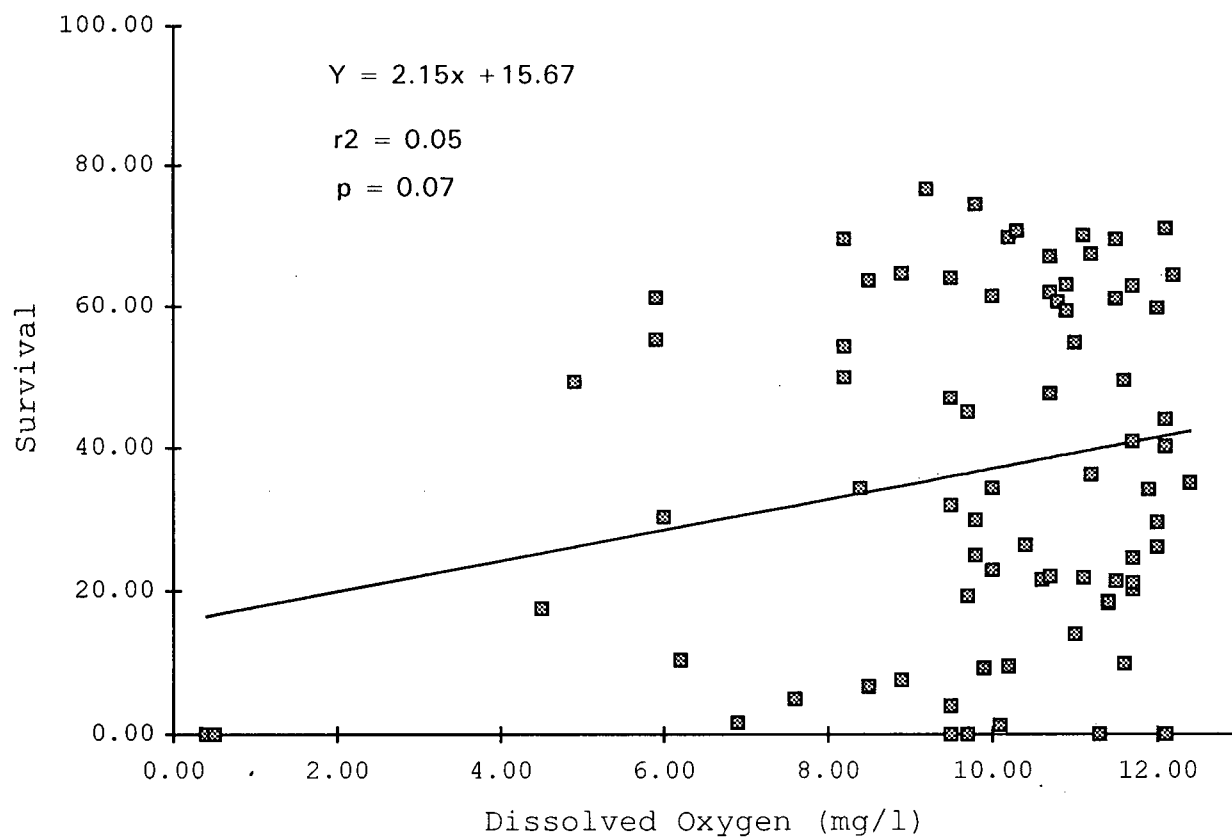
Figure 14. Linear regression of the 1994 embryo survival rate
(all creeks, locations) 50 days after fertilization on the
corresponding intragravel dissolved oxygen (@ 20 cm depth) at
the period immediately prior to egg deposition.

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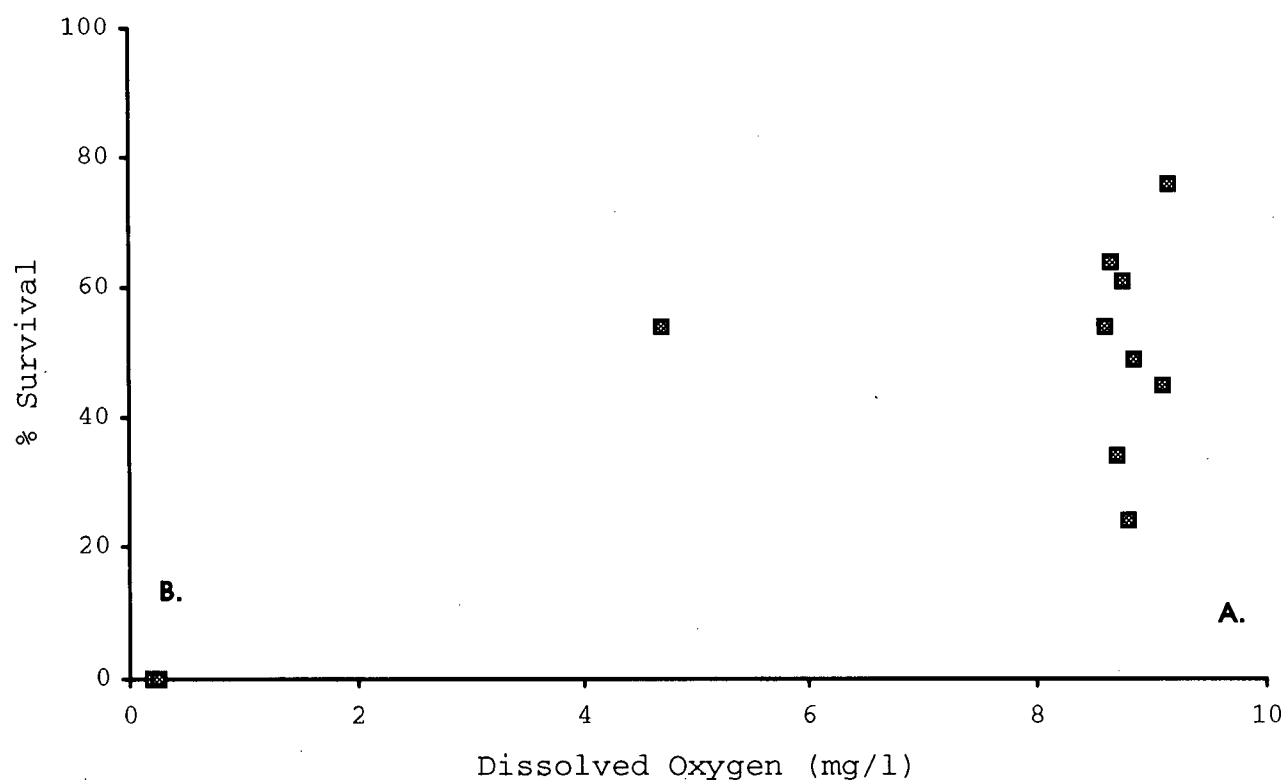
Figure 15. The 1994 embryo survival rate (%) from the transect experimental reach (Kynock 1550 m site; Appendix A) 50 days after fertilization versus the corresponding intragravel dissolved oxygen (@ 20 cm depth) at the period immediately prior to egg deposition. Transect runs from the north bank margin (A) across a riffle and pool into the off-channel habitat (B).

47

(Fig. 16). The non-random temporal selection of incubation sites led to a negative relationship between the date of fertilization and the resulting survival 50 days after fertilization. The temporal sequence of fertilization and capsule implantation was Kynock, Forfar, Gluskie, and Bivouac creek. Temporal sequence was dictated by the order of spawning and maturation within spawning streams. This relationship between date of fertilization and survival rate was not evident in 1993 under a similar temporal sequence. The negative relationship of 1994 coincides with the period when escapement unexpectedly dropped off (Fig. 4). This relationship was exemplified within Kynock Creek study reaches. Gametes collected on August 4-6, 2-4 days after the escapement peak, had some of the highest survival rates (Fig. 16). On August 9, 7 days after the end of the escapement peak, gametes were stripped from the few remaining ripe adults at the fence. Although these embryos were planted within the same location they had significantly lower survival rates (Fig. 16). Embryos collected on August 9 suffered a mortality event at stage 8-10. This coincides with 20-60 ATU's or 2-10 days post-fertilization. This mortality event was not evident in gametes collected on August 4-6 and incubated within the same stream reach.

Alevin Development and Behaviour

Table 4 summarizes the physical characteristics of stranded (marginal sites subject to exposure) and control (preferred) *in situ* redd simulations. There was no difference in intragravel

48
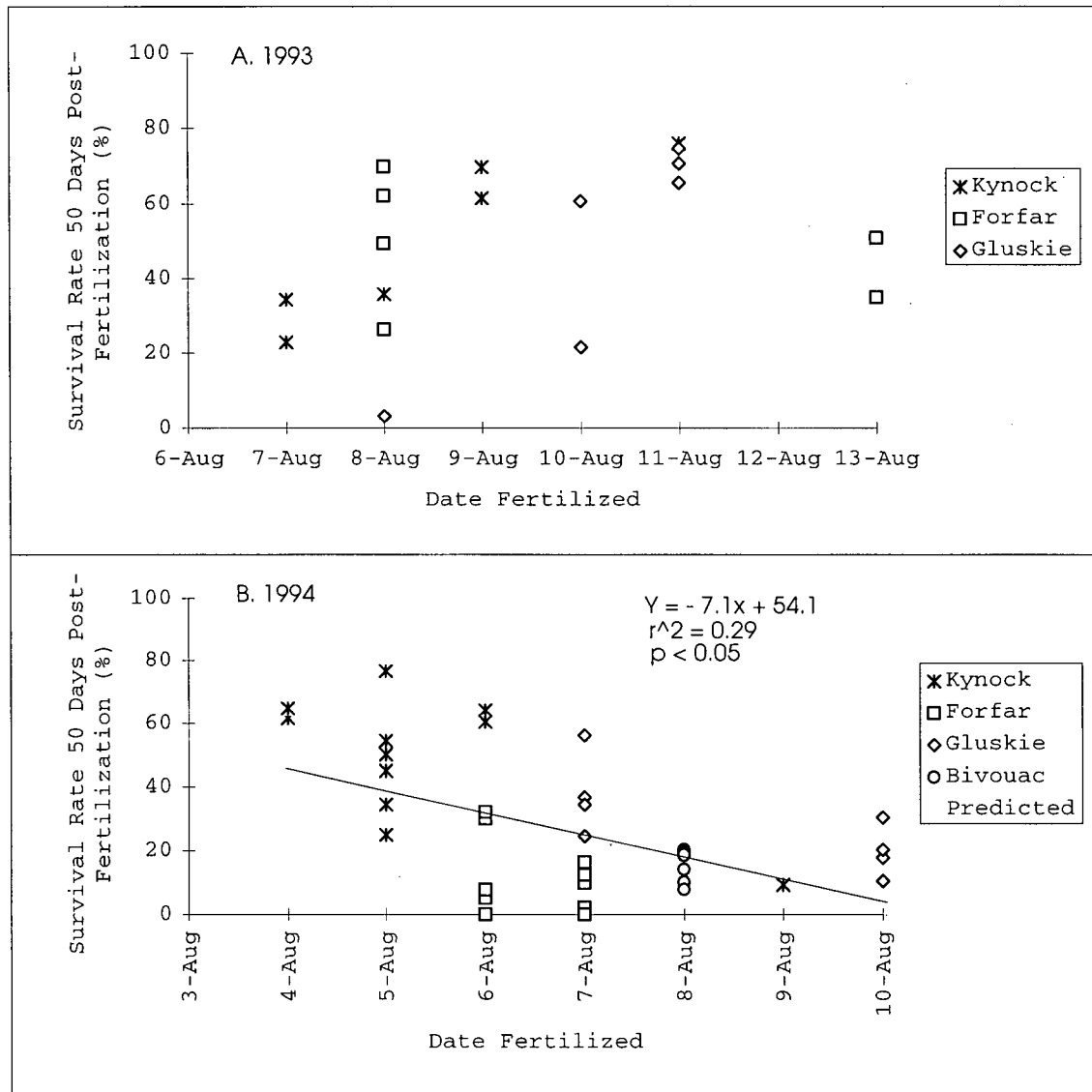
Figure 16. Mean capsule survival rate (50 days post fertilization) for fertilization procedures by date fertilized and creek. A. 1993 fertilization batches and corresponding survival rates. B. 1994 fertilization batches and corresponding survival rates.

49

Table 4. Summary of stream and intragravel physical parameters and corresponding embryo survival rates for *in situ* redd stranding simulations and preferred (control) redd simulations. Embryos were fertilized and incubation capsules planted in late August. Experiment was terminated in mid-February under seasonal minima conditions for discharge and temperature.

Variable	Sample Period	REDD SIMULATION							
		Kynock 1550 m		Kynock 300 m		Forfar 150 m		Forfar 1500 m	
		Stranded	preferred control	Stranded	preferred control	Stranded	preferred control	Stranded	preferred control
Intragravel Dissolved Oxygen (mg/l)	July	9.1	8.7	9.1	8.2	9.4	9.6	9.7	10.1
	Sept	9.2	10.0	9.0	9.5	9.0	9.8	9.6	8.9
	Feb	**11.3	8.5	–	–	–	–	**8.6	12.4
Intragravel Temperature (deg C)	July	12.8	12.5	12.2	12.4	10.6	10.6	11	10.3
	Sept	7.7	7.5	9.5	9.4	8.3	8.3	9.3	9.2
	Feb	**0.0	0.1	–	–	–	–	**0.3	0.0
Water Depth Above Substrate (cm)	July	8	42	12	17	14	10	7	50
	Sept	8	32	6	26	2	25	3	27
	Feb	-40	*25	-2	*20	-15	*15	-15	*25
Stream Velocity (m/s)	July	0.68	0.40	0.12	0.15	0.42	0.30	0.30	0.55
	Sept	0.02	0.17	0.02	0.25	0.22	0.09	0.01	0.16
	Feb	0.00	–	0.00	–	0.00	–	0.00	–
Intragravel Depth of Freezing (cm)	Sept	–	–	–	–	–	–		
	Feb	40	0	2	0	15	0	20	0
Mean Survival (%) (Standard/behaviour)	Feb	0 /39	64	16/13	60	32/34	32	0/0	2

Note: unable to retrieve Gluskie 50 m redd stranding simulation

* = visual estimate

**=40 cm deep standpipe

September sample period =eyed egg (56 days post fertilization)

February sample period =alevin (185 days post-fertilization)

dissolved oxygen (p>0.05). Samples taken at a depth of 40 cm (11.3 mg/l, 8.6 mg/l) indicate hospitable rearing environments at depths below the mean redd depth of 20 cm. No control sites were subject to desiccation or freezing (waterlevel above surficial substrate). All of the stranding simulations were influenced by declining waterlevels. Embryos within standard capsules, within a stranded redd, survived unless the depth of freezing penetrated to the bottom of the capsules (Table 4). The vertical distribution of alevins within behaviour capsules in relation to depth of freezing confirms alevins are responding directly to this stimulus rather than to some other factor that might promote better survival by moving deeper into the gravel (Fig. 17).

Comparison of the estimated hatching interval (Fig. 18) and stream thermograph (Fig. 9) suggest alevin hatching coincides with the mean time of the fall freeze-up. Spawning coincides with maximum annual stream temperatures and incubating embryos rapidly accumulate thermal units early in development. As a result 67% of the thermal units are accumulated within the first 19% of the incubation period (Fig. 18). Hatching was estimated to occur between Sept 27 - Oct 29. Embryonic stage in late September ranged from stage 24 (primordial caudal fin, 3/4 yolk sac vascularized) to stage 30 (hatched alevin). The range of thermal units at this point was 372-436. By early December, during the onset of minimum temperatures and flows, 100% of embryos had reached the alevin stage (stage 31-35). Coinciding with rising stream temperatures in spring, fry emergence occurs principly from mid-April to mid-May

51

A.

B.

C.
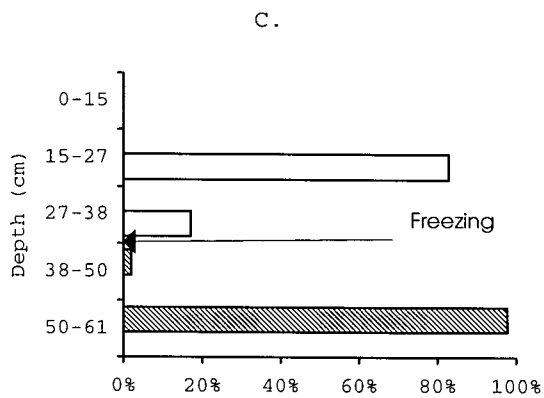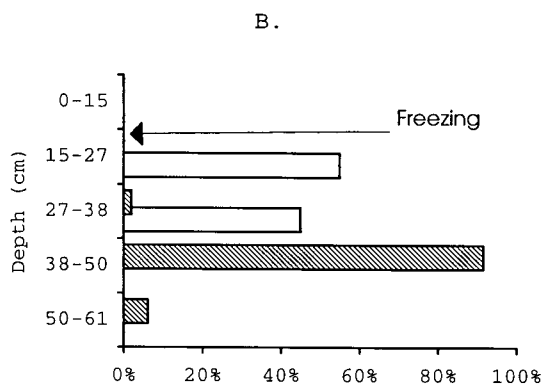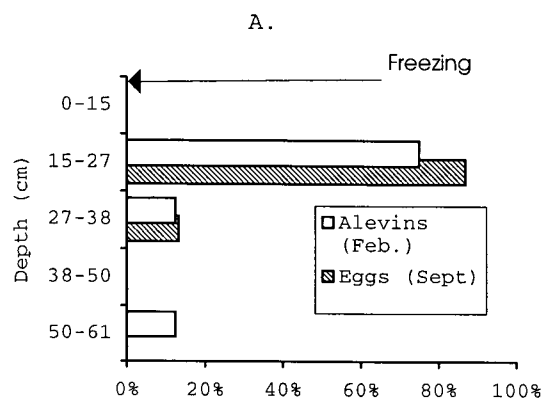
Percent total larvae

Figure 17. Intragravel pattern of changes in vertical distribution
of sockeye alevins in relation to depth of freezing. A. 2 cm
depth of freezing within substrate. B. 15 cm. C. 40 cm.

52
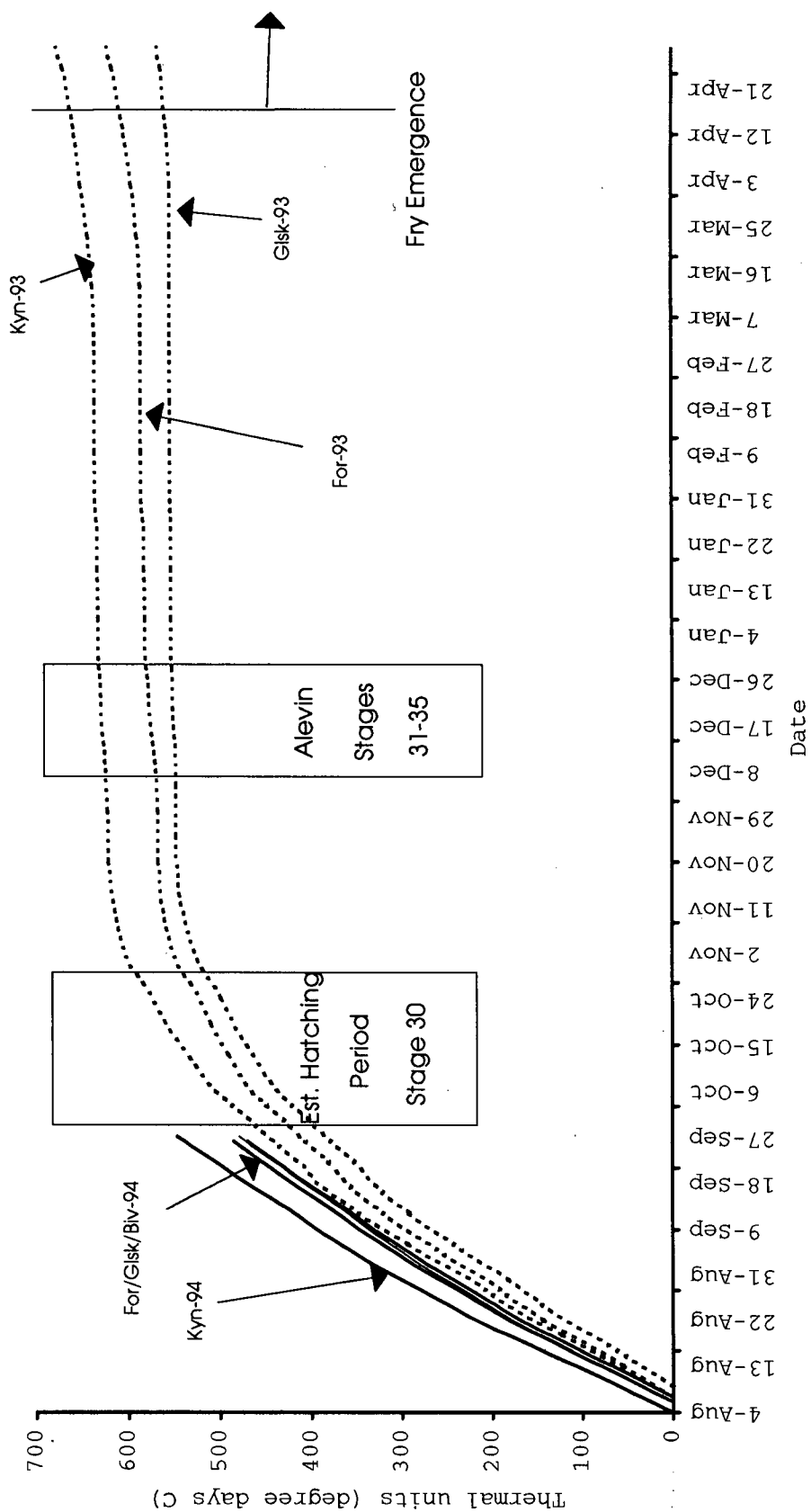
Figure 18. Accumulated mean daily temperature units (CTU) observed for the two years of incubation study within Kynock, Forfar, Gluskie and Bivouac creeks. Temperature data was from B. Anderson, D.F.O., P.B.S., unpubl. data. Developmental stages were determined from capsule embryos retrieved in Late September, Mid-December, and mid-April utilizing the classification system of Vernier (1969).

53

after exposure to 600-800 thermal units (mean = 260 days).

CHAPTER 4 - DISCUSSION

The stock concept of "unique" salmon "races" (Larkin 1972, Ricker 1973) is important to management of Pacific salmon, and the Fraser River sockeye are composed of a multitude of local spawning stocks (Killick 1955, Gilhousen 1960, Cass 1986). While we know very little about the genetic composition of the individual spawning stocks, it is widely believed that differences in reproductive and developmental biology among populations must reflect adaptations to the specific environmental conditions experienced during spawning and development (Miller and Brannon 1982, Brannon 1987, Beacham and Murray 1989, 1990, Murray and McPhail 1988, Murray et. al. 1989, 1990).

Developing an understanding of how incubating embryos survive through seasonal variation in temperature and hydrologic regime was a priority of this project. Observed survival rates were facilitated by; 1) spawning adults selecting incubation microhabitat to optimize egg to fry survival and, 2) a number of general mechanisms which would optimize incubation success in northern environments. These mechanisms included; the early time of spawning, thermal tolerance, development rate, alevin behavioral mechanisms, and habitat modifications by spawning adults. I will discuss those characteristics of the environment and population which directly relate to incubation survival in northern environments. I reject the anthropocentric view that northern incubation streams are a harsh and unforgiving incubation

environment and that prophylactic measures (i.e. spawning channels) are necessary to mitigate over-winter mortality.

Spatial preferences

Micro-Habitat

Although the environment ultimately determines if a fertilized egg will survive to produce a fry, the opportunity to survive may be influenced by the behaviour of the parents. Of special significance is the distribution of spawners on the spawning beds. Preferred habitat was the downstream ends of pools at the pool riffle interface. Numerous studies have previously documented this habitat preference for salmonids (Stuart 1953, Hunter 1959, Cooper 1965, Vaux 1968, Hoopes 1972, Tautz and Groot 1975, Reiser and Wesche 1977, Thurow and King 1994). Marginal habitats which were utilized to a lesser degree included; riffles, stream margins, intermittent side channels and portions of the off-channel habitat.

Sockeye successfully spawned over a wide range of habitats. This range likely has upper and lower limits beyond which fish were unwilling to spawn as observed from the lack of spawning in habitat where intragravel dissolved oxygen levels were below 3.0 mg/l. Based on the lineal distribution of spawning adults and their corresponding micro-habitat parameters, few locations in the lower and mid-watershed reaches contained these "zones of exclusion" (Tschaplinski 1994) .

Distribution on the spawning grounds

Due to the fortuitous timing of this study a high density year (3.46 spawners/m^2) was followed by a very low density year (0.30 spawners/m^2). In 1993, during historic high escapements, there were much higher local spawning densities in preferred and marginal habitats. However, the poor quality habitats (i.e. dissolved oxygen <3.0 mg/l) were generally not utilized for spawning even in this situation. Instead, a larger scale spatial re-distribution of spawners occurred. First, ranges within the creeks were expanded to limits imposed by upstream obstructions. This resulted in estimated escapement capacities (Langer et. al. 1992), being met or exceeded. Secondly, spawner escapement estimates of alternative tributaries reached unprecedented levels (i.e. Bivouac, Leo creeks), and were well beyond previously described ranges within most other natal streams (G. Smith, D.F.O., Stock Assessment Group, per. comm.). This escapement re-distribution in dominant cycle years was a previously noted phenomenon of the early Stuart stock (J. Woodey, D.F.O., per. comm, Langer et. al. 1992) and Alaskan sockeye stocks (Blair and Quinn 1991).

The over-representation of escapement to the study streams indicate spawners are preferentially selecting these streams. Results from the gamete transplant experiment between study streams suggest this stock was not prevented by specific stream selection regimes from colonizing other streams within the Stuart/Takla watershed. Previous displacement experiments of sockeye from small streams within a lake system suggest attraction

to certain spawning site characteristics and conspecifics on a local scale, rather than site specific homing (Blair and Quinn 1991).

To summarize, results from this study and the literature suggest spawning adults select spawning habitat to optimize egg to fry survival. Once local densities reach certain limits the remaining spawners, as predicted by the gradation in habitat model (Hilborn and Walters 1992) and density-dependent habitat selection model (MacCall 1990), move on to colonize less densely populated reaches or streams rather than spawn in unsuitable habitat, or at dangerously high densities on a local scale.

Incubation Survival

The survival rate to pre-emergent fry reflects the overall rigors endured by a given population of developing eggs and alevins and is a consequence of the severity of the environmental conditions and the adaptability of the fry (Koski 1975). The capability of these northern interior streams to sustain eggs and alevins from fertilization to pre-emergence was inferred from the results using the perforated incubation capsules. These bioassays are designed to indicate the quality of spawning habitat for the embryo and alevin stage of incubation. They do not provide an assessment of the critical stage of alevin to emergent fry.

Mean survival rates to pre-emergent fry of 49% and 28% for 1993 and 1994 respectively, are indicative of a high quality incubation habitat. Productivity, related to density-independent

mechanisms, for Kynock, Forfar and Gluskie creeks appears to be very high. Egg to pre-emergent fry survival rates ranged from 16-60%. This compares favourably to pre-emergent fry survival rates for similar studies (*Oncorhynchus* spp.) in coastal systems; 0-87% (Phillips and Campbell 1961), 16-62% (Coble 1961), 3-47% (Scrivener 1988), and 0-67% (Groot 1989). Other investigators (Hunter 1959, McNeil 1962) reported pre-hatch mortality rates commonly exceeding 90% under natural conditions. Further, the early Stuart stock does not exhibit lower overall recruitment rates per spawner than other Fraser River stocks (Walters and Staley 1987, Cass 1989).

Much of the mortality in spawning beds has been attributed to the inability of fry to emerge from the gravel (Koski 1966, 1975, Phillips et. al. 1975). Therefore, studies in which the newly emerged migrant fry are counted as they leave the stream may give a more accurate estimate of fry production within a stream. Survival of Pacific salmonids to emergence under natural conditions is highly variable but normally low; coho 23%-27% (Chapman 1965, Koski 1966), chum 6-31% (Cowan 1991), and pink salmon seldom exceed 20% (Hunter 1959, Parker 1962, McNeil 1966). Estimated fry survival for sockeye salmon also appears low and has ranged from 2 to 25% over a period of several years in several streams (Fish. Res. Bd. Can. 1956), 11-31% in Fulton River (Anon 1968), and 8.9 -17.1% in Meadow Creek (Kokanee, Taylor et. al. 1972). Concurrent egg to emigrating fry estimates within the study streams during the two years of this study ranged from 12-48% (G. Smith, D.F.O., Stock

Assessment Group, unpubl. data). These egg to fry survival rates were higher than other sockeye stocks within the juvenile enumeration program (G. Smith, D.F.O., Stock Assessment Group, per. comm.). The combination of high incubation survival rates, low over-winter mortality rates, and the high fry production estimates, support the conclusion that these streams are high quality incubation streams.

Very often spawners are too few to occupy fully the available spawning area. It has been argued that areas not used when runs are small have relatively poor conditions for eggs and alevins (Hunter 1959). Results from this study do not support this contention. The upper Gluskie Creek incubation site was not utilized during the low escapement year, yet provided some of the highest survival rates within this creek. Merrell (1962) and McNeil (1968) reported a similar phenomenon with pink salmon in southwestern Alaska. Stock recruitment analysis also does not support the contention that different cycle lines are significantly different in productivity (Walters and Staley 1987, Cass 1989, Blair and Quinn 1991). During this study, densities were an order of magnitude different, yet produced similar mean egg to emigrating fry survival rates (Table 1). The higher fry production estimates of 1994 appears to contradict that of the pre-emergent survival estimates. I speculate that the higher early mortality rates observed within incubation capsules were compensated for by a dramatic decrease in superimposition at the much lower spawner densities of 1994.

Effects of Environmental Factors on Incubation Survival

Survival rates between preferred and marginal habitats were not significantly different in contrast to predictions generated from optimality models (Fretwell and Lucas 1970, MacCall 1990, Hilborn and Walters 1992). This was due to the perception and definition of "marginal" habitat. Truly marginal areas (i.e. < 3.0 mg/l dissolved oxygen) were avoided by spawning adults. The result was low density (i.e. assumed marginal) and high density (i.e. assumed preferred) *in situ* redd simulations with similar intragravel conditions.

Temperature and Embryo Development

The first habitat limitation of concern was maximum stream temperatures during spawning. Mean stream spawning period temperatures ranged from 10.2 - 13.4°C. Intragravel temperatures closely followed these values. While mean spawning period temperatures were below maximums reflected in the literature for successful spawning and fertilization, daily maximum temperatures approached 16°C in Kynock Creek in 1994. Mortality was not significantly related to spawning period temperatures. Contrary to expectations the highest survival rates were associated with the highest temperatures.

The second limitation of concern was over-wintering egg mortality due to freezing and dewatering. Stream temperatures declined to mid-winter lows of 0°C for several months, and water levels declined to ≈20% of spawning period (Scrivener and Anderson

1994). However, the majority of mortality (80%) occurred before the onset of winter conditions, and only 12% of embryo mortality occurred from 10 Oct - 15 April (Fig. 6). These results conform to patterns derived for *Oncorhynchus* spp. from coastal and laboratory systems (Wickett 1954, Alderdice et. al. 1958, Hunter 1959, McNeil 1962, Murray and McPhail 1988, Beacham and Murray 1989). This suggests over-winter mortality due to freezing and desiccation was not determining fry production as originally hypothesized.

The characteristic signature of groundwater upwelling in a northern environment is a warmer, more stable winter thermal regime within the intragravel environment (Sheridan 1962, Cooper 1965, Leman 1993). Where intragravel water temperatures differ only a small amount from the stream, the major source of intragravel dissolved oxygen is the interchange of that water with surface flow (Sheridan 1962, Cooper 1965). Study streams were indicative of high interchange between stream and intragravel environment. This indicates the incubation environment is maintained by the stream and not upwelling groundwater. Therefore, spawning salmon were not selecting incubation sites based on temperature (i.e. upwelling groundwater to maximize embryo survival rate).

In the case of fall spawners the embryos must reach some critical stage of development before the water becomes to cold (Brannon 1965). Results from Combs and Burrows (1957) and Combs (1965) suggest that pink and chinook embryos could tolerate long periods of low temperatures if the initial temperature was above 6.0°C and embryogenesis had proceeded to a critical developmental

stage. The early Stuart stock spawns four weeks earlier than any other Fraser River stock (Killick 1955, Brannon 1987), allowing incubating embryos to rapidly accumulate thermal units and reach this critical stage prior to winter "freeze-up".

Results in experimental channels and simulated redds indicate eggs can tolerate 1-5 weeks dewatering with no effects on hatching success, provided moisture content is maintained and the sediments neither freeze nor exceed incubation tolerances (Fast et. al. 1982, Becker et. al. 1983, Reiser and White 1983, Neitzel and Becker 1985, Becker et. al. 1986). Newly hatched alevins, however, are intolerant due to the formation of functional gills (Becker et. al. 1982). By spawning earlier than any other sockeye stock the early Stuart adults ensure embryos experience a rapid early development phase and are undergoing the critical hatching phase as freeze-up descends upon the region.

Salmonid alevins move about both laterally and vertically within the gravel bed prior to emergence, and changing environmental conditions may affect subgravel behaviour (Stuart 1953, Dill 1967, 1969, Bams 1969, Dill and Northcote 1970, Carey and Noakes 1981, Godin 1982, Fast et. al. 1982, Garcia De Leaniz et. al. 1993). Frequent movement, in favourable substrata, of 5 cm/min has been recorded (Bams 1969). The observed downward migratory response of sockeye alevins to freezing (Fig. 17) is an adaptation to the incubation environment. This mitigates the apparent harshness of interior streams. Laboratory results utilizing early Stuart broodstock duplicated these *in situ*

63

results (Dr. M. Bradford, D.F.O., Research Division, per. comm.).
Directed movement was found under temperature stress, but not in
controls, confirming that alevins are responding to temperature.
This response was not observed in coastal chinook alevins
indicating either: 1) There was an interaction between substrate
size and alevin size which allowed the sockeye alevins to migrate
and not the larger chinook. 2) There is a genetic determinant of
behaviour, which the coastal chinook alevins lacked.

Gravel Quality and Dissolved Oxygen

Numerous studies have led to consensus that low dissolved
oxygen and reduced water exchange increase embryo mortality.
Variation due to other factors often obscures this relationship in
natural systems, such that survival often appears independent of
intragravel dissolved oxygen (Koski 1966, Chapman 1988, Groot 1989,
Vronskii and Leman 1991). Hansen (1975) found streambed areas with
low dissolved oxygen (< 3.0 mg/l) were not used for spawning.
Ninety percent of the intragravel dissolved oxygen values within
this study were > 6.0 mg/l. Those areas below 3.0 mg/l were not
utilized for spawning. As a result, it should not be surprising to
find there was not a significant relationship between intragravel
dissolved oxygen and survival.

Survival of salmonid embryos has been related to substrate
composition in many experiments and field studies (Koski 1966,
1975, Tappel and Bjornn 1983, Tagart 1984, Scrivener and Brownlee
1989, Lisle and Lewis 1992, Hall and Lantz 1969, Dill and Northcote

64

1970). High intragravel dissolved oxygen and survival rates have often been attributed to high permeabilities (Coble 1961, Wells and McNeil 1970, Wickett 1970). Permeability does not affect survival directly but is a measure of the adequacy of the gravel in the redd to allow for a sufficient supply of water and dissolved oxygen to the embryos and fry.

The spawning female can alter grain size and porosity of gravel to ensure that ova begin with an adequate flow of oxygenated water (Chapman 1988). Vigorous digging of the female removes fines and small gravels to form the egg pocket and the completed redd contains less fine silt and sand than the surrounding substrate (McNeil and Ahnell 1964, Ringler 1970, Everest et. al. 1987, Chapman 1988). Substrate permeabilities within the study streams closely agree with values documented by Chapman (1988) for heavy spawning gravel beds of optimal survival conditions. Concurrent studies by other researchers demonstrate that particles < 0.3 mm in diameter were rare (1-1.6%) and interstitial spaces in the gravel would remain clear permitting water exchange and movement of alevins (Scrivener 1994). The lowest mean permeabilities at the completion of the incubation period were > 19 ml/s (Table 3). Koski (1966) reported no detectable affect on survival above this threshold. Egg to fry survival rates of > 30% are expected from such gravels (Lotspeich and Everest 1981, Scrivener and Brownlee 1989, Chapman 1988, Scrivener 1994).

Large annual spawning populations of Pacific salmon probably engender a "mass cleaning" and help maintain high quality spawning

65

habitat (Everest et. al. 1987, Chapman 1988, Burgner 1991). Annual scarification of flow controlled spawning channels is a commonly used remedial measure to mimic this effect (Taylor et. al. 1972). Using independent methods, Scrivener and Anderson (1994) and Gottesfeld (1994), estimated spawning salmon within the study streams accounted for 25-50 % of the annual movement of bed material. During salmon spawning, over-representation of fine sediments (<1.19mm) in bedload movement, in conjunction with a suspended sediment concentration peak, suggest spawners were measurably influencing the particle size distribution of the streambed (Scrivener and Anderson 1994). It is possible that over the course of a number of years the geomorphic work done by spawning sockeye is comparable to or even greater than that performed by floods (Gottesfeld 1994).

Interior systems have low autumn and winter stream flows. These flows are unable to transport bedload and do not form a layering pattern like coastal systems, where spawning takes place as autumn and winter freshets are establishing layering patterns (C. Scrivener, D.F.O., Research Division, per. comm.). As a result, interior spawning sockeye salmon have a lasting impression on the streambed characteristics.

Stress

Production of fry under optimal conditions (i.e. artificial spawning channels) is not constant from year to year or from stream to stream, and the differences often remain unexplained. A critical

66

question of sockeye salmon population biology is the relative importance of stress factors encountered by spawners prior to spawning, versus stress felt by embryos due to the environmental conditions experienced during incubation.

The early Stuart stock enters the Fraser River from late June through mid-late July at a time when river temperatures are rising and the flows are near their peak (Clarke et. al. 1994). This combination of high temperatures and high streamflow during the migration period can place severe demands on energy reserves, resulting in the utilization of 90-95% of body fat reserves and 55-60% of protein reserves (Idler and Clemens 1959).

The incubation capsule results in 1994 demonstrate a negative relationship between date fertilized and survival rate. Furthermore, embryos within the same location (Kynock 300 m) had very different survival rates based on the date gametes were stripped and fertilized. This indicates a possible deterioration of gamete viability. This relationship coincided with dates when escapement unexpectedly dropped off during the second half of the run (Fig. 4). Evidence of an early mortality event in the late spawned gametes and not the earlier gametes, in conjunction with no known change in physical incubation conditions, indicate factors other than environmental conditions may have been responsible.

It has been hypothesized that the decline in arrivals was coincidental with, and caused by, the extreme temperatures that developed in the Fraser River during the 1994 migration (Fig. 19; Clarke et. al. 1995). The 1994 early Stuart migration temperature

began slightly below average and rapidly rose at peak passage time to reach historical maximum levels. Ocean conditions set the stage for successful river migration (Blackbourne 1991, Mysak 1986, Hinch et. Al. 1994, 1995). Analysis of weight-length regressions (Dr. S. Hinch, U.B.C. Fisheries Centre, pers. com.) indicated the 1994 early Stuart sockeye were in better initial condition than the 1993 broodstock. Bioenergetic modelling indicated that energy use in 1994 was the third highest recorded while 1993 was equivalent to the long term average (Clarke et. al. 1995). In 1993 79% of radio-tagged sockeye reached Hell's Gate, while in 1994 67% arrived. However, during the second week of July (1994) as temperatures rose rapidly, no fish reached Hell's Gate, and fish still downstream displayed erratic behaviour (Clarke et. al. 1995). It has been demonstrated that elevated water temperatures during upstream spawning migrations create severe and acute stress which alters behavioral and physiological responses (Johnston et. al. 1992). Killick (1955) demonstrated the chronological order of sockeye migration, spawning and death show remarkable consistency within races. The abrupt disappearance of the tail of the run at the spawning grounds supports these findings.

The hypothesis that migration arduousness may affect progeny survival was incidently tested in this study. The historical mean recruits per spawner database (1949-1987; Pac. Salm. Comm., unpubl. data) was blocked by 1°C increments of mean July temperature at Hell's Gate. There appears to be an optimum temperature range for progeny survival from broodstock migration at 15-16°C (Fig. 20).
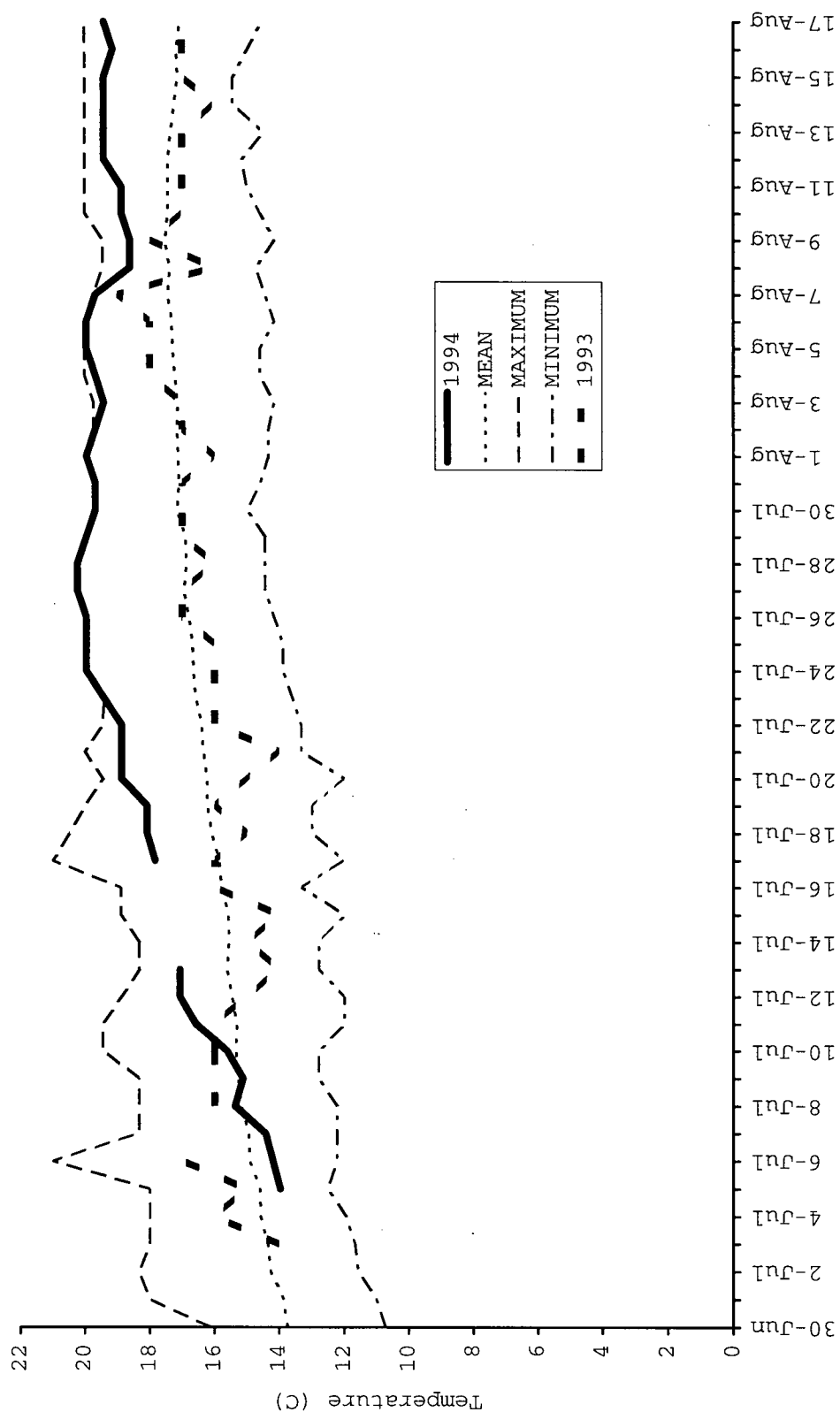
Figure 19. Daily maximum, minimum and mean water temperatures from the Fraser River at Hell's Gate (average from 1945 - 1993), compared with the 1993 and 1994 mean daily temperatures.
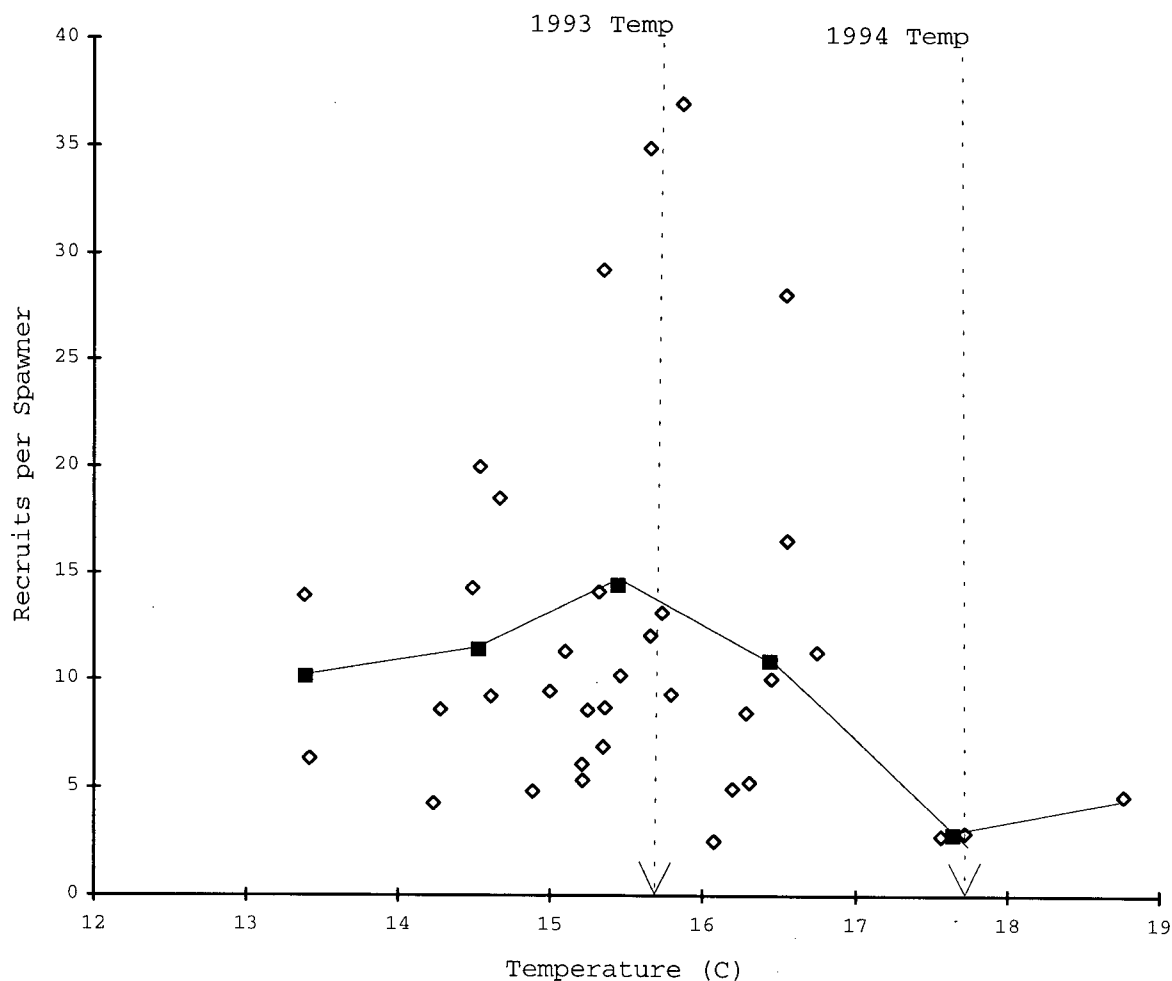
Figure 20. Mean early Stuart recruits per spawner for each one
degree celsius increment of mean July Fraser River water
temperature at Hell's gate for the period 1948 - 1989.
Recruits per spawner calculated from INPFC sockeye database
(I. Williams, D.F.O., P.B.S, unpubl. data) based on returns
calculated from estimated catch plus escapement on a four year
return cycle. Mean July Fraser River water temperature
calculated for each corresponding year from Hell's Gate
database.

70

How egg quality affects embryo survival is at this point just conjecture. Advancing temperature above species specific optima during the spawning migration appears to have an inhibiting effect on gonad development and gamete quality in many salmonid species. Columbia River sockeye lose an average of 7.5% of their body weight at 10°C and 12% at 16.5°C. Testes were > 25% smaller at 16.5°C, and adverse gonadal development was evident in females who produced smaller and lighter eggs at 16.5°C (Bouck et. al. 1975, Bouck 1977). In 1977 approximately 6 347 000 eggs were stripped from moribund Horsefly females (INPFC 1978). Fry production was estimated at just 0.3% (INPFC 1979), and viability of the eggs was the suspected cause. Chronic confinement and acute emersion stress results in endocrine dysfunctions and significantly lower survival rates (fertilization to 28 days posthatch) for progeny from stressed fish compared to progeny from unstressed control fish (Campbell et. al. 1992, 1994).

While the fish culture industry recognizes that varying egg quality is one of the limiting factors for successful mass production of fish fry (Piper et. al. 1982, Kjorsvik et. al. 1990), classical recruitment models (Ricker 1954, Beverton and Holt 1957, recruitment regression models) have not explicitly recognized the effects of egg quality on survival of potential recruits. Such models have generally assumed that variation in recruits per spawner must be due to variations in environmental conditions experienced by the recruits, not their parents. My hypothesis suggests migration conditions encountered by adult sockeye in the

mainstem Fraser River may determine the year class strength of the progeny. Therefore, egg production and juvenile environmental conditions alone cannot be relied upon as predictors of reproductive success.

CHAPTER 5 - CONCLUSION

The high productivity, related to density-independent mechanisms, for the spawning grounds of these central interior study streams was inferred from results using perforated incubation capsules. The combination of high incubation survival rates, low overwinter mortality rates and the high fry production estimates, support the conclusion that these streams are high quality incubation streams.

Several factors resulted in the lack of classical relations observed in previous studies between incubation parameters and survival. Observed survival rates were facilitated by spawning adults selecting incubation microhabitat to optimize egg to fry survival. Survival rates between low density and high density spawning habitats were not significantly different due to the perception and definition of "marginal" habitat. Truly marginal areas were avoided by spawning adults. The result was low density (i.e. assumed marginal) and high density (i.e. assumed preferred) *in situ* redd simulations with similar intragravel conditions.

Incubation environments were relatively invariant with high quality incubation habitat available at all scales examined. It was proposed that the relatively uniform, high quality habitat was due to; 1) the high quality of available bedload, of the correct dimensions, that moves through these systems at a rate that is modest in comparison to coastal systems and, 2) the mass cleaning engendered by high densities of spawning adults. This results in

73

high quality gravel conditions with permeabilities, surface water interchange, and intragravel dissolved oxygen levels associated with high incubation success.

A number of mechanisms to optimize incubation success in northern environments were identified within the early Stuart stock. Early Stuart sockeye risk energy depletion and seasonal maximum temperatures during migration and spawning. The advantage accrued by spawning early in the season is advanced embryological development prior to the onset of low water temperatures. Embryos rapidly accumulate the thermal units necessary to hatch, thereby becoming mobile in time to respond to freezing and desiccation as water-levels decline. Alevins of the early Stuart stock can apparently tolerate temperature conditions previously considered lethal for long periods of time and emerge successfully after less thermal units than any other Fraser River stock.

The trade off against this strategy is the effect of unusually stressful migration conditions on the quality and viability of the gametes. Evidence of this trade off was obtained in 1994 when egg survival rates were very low for spawners that arrived late and had suffered severe thermal stress during migration. Implications for stock management are the general assumption of classical recruitment models that variation in recruits per spawner must be due to variations in environmental conditions experienced by the recruits, not their parents. Implications to habitat management include; 1) the seasonal variation in temperature and discharge during spawning and incubation and, 2) increases or changes in the

character of sediment input. As spawning period temperatures approach critical levels and energy reserves of spawning adults are at a minimum, riparian forestry prescriptions must be closely monitored. The apparent adaptation in developmental biology of the early Stuart stock and the specific timing to the seasonal variation in temperature and hydraulic regime would suggest monitoring of these variables in association with forestry prescriptions should be a priority of future research. As riparian zone substrates are characterized by large amounts of lacustrine deposits post-logging increases in the delivery of fine sediments must not surpass the ability of physical (hydraulic regime, bedload characteristics) and biological (mass cleaning by high densities of spawning adults) processes to maintain the current gravel quality.

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APPENDIX A

Schematic representations of study reaches showing
standpipe monitoring stations, egg incubation sites
(redd simulations), and observed redd distribution.

Figure A1. Kynock Creek mid-watershed (1550m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution.

LEGEND

- ○ Permanent Transect Stake
- ● Standpipe Monitoring Station
- "Preferred" Habitat Redd Simulation
- "Marginal" Habitat Redd Simulation
- "Stranded" Redd Simulation
- Incubation "Bag" Redd Simulation
- Gamete Transplant Incubation Site
- □ Transect Incubation Site
- 93 Observed Sockeye Redd (1993)
- 94 Observed Sockeye Redd (1994)

N

FLOW

POOL

RIFFLE

GRAVEL BAR

OFF-CHANNEL

POOL

SCALE
(meters)
0   5

Figure A2. Kynock Creek lower-watershed (350m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution.

FLOW

POOL
1

N

OFF-CHANNEL

T1
T2
T3
T4

3
2
2A
4
5
6
7
7A
8
9
10
11
12

GLIDE

Gravel Bar

RIFFLE

Gravel Bar

POOL

SCALE
(meters)

0   5

LEGEND

○ Permanent Transect Stake
● Standpipe Monitoring Station
▓ "Preferred" Habitat Redd Simulation
░ "Marginal" Habitat Redd Simulation
▓ "Stranded " Redd Simulation
▒ Incubation "Bag" Redd Simulation

⑨③ Observed Sockeye Redd (1993)
⑨④ Observed Sockeye Redd (1994)

93

Figure A3. Forfar Creek mid-watershed (1500m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution.

N

FLOW

POOL

OFF-CHANNEL

GLIDE

GRAVEL BAR

RIFFLE

SCALE
(meters)

0   5

LEGEND

○ Permanent Transect Stake
● Standpipe Monitoring Station
▦ "Preferred" Habitat Redd Simulation
▢ "Marginal" Habitat Redd Simulation
▨ "Stranded " Redd Simulation
▦ Incubation "Bag" Redd Simulation
■ Gamete Transplant Incubation Site
▢ Transect Incubation Site
㉛ Observed Sockeye Redd (1993)
㉞ Observed Sockeye Redd (1994)

94

Figure A4. Forfar Creek lower-watershed (150m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution.

Figure A5. Gluskie Creek mid-watershed (400m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution.

LEGEND

○ Permanent Transect Stake
● Standpipe Monitoring Station
▨ "Preferred" Habitat Redd Simulation
▨ "Marginal" Habitat Redd Simulation
▨ "Stranded " Redd Simulation
▨ Incubation "Bag" Redd Simulation
▨ Gamete Transplant Incubation Site
☐ Transect Incubation Site
�93 Observed Sockeye Redd (1993)
�94 Observed Sockeye Redd (1994)

SCALE
(meters)

0   5

96

Figure A6. Gluskie Creek lower-watershed (50m) study reach showing standpipe monitoring stations, egg incubation sites (redd simulations), and observed redd distribution. (note redd observations were not recorded in 1993. Standpipe monitoring station locations varied between years due to beaver dam.)

SCALE
(meters)

0   5

LEGEND

○ Permanent Transect Stake
● Standpipe Monitoring Station
▨ "Preferred" Habitat Redd Simulation
▫ "Marginal" Habitat Redd Simulation
▨ "Stranded " Redd Simulation
▨ Incubation "Bag" Redd Simulation
■ Gamete Transplant Incubation Site
□ Transect Incubation Site
⊘ 93 Observed Sockeye Redd (1993)
⊘ 94 Observed Sockeye Redd (1994)

APPENDIX B

Summary of egg to pre-emergent survival rates for
preferred and marginal redd simulations

Appendix B1. Summary of mean survival rate ($n_{1993}=10$, $n_{1994}=6$-7 capsules per site/time retrieval) for incubation habitat type (preferred=high utilization, marginal=low utilization) by creek (n=4), location (upper=mid-watershed, lower=lower watershed), and sample session (developmental stage; 1=late September, 2=late December, 3=late April) for selected spawning streams of the early Stuart sockeye stock. Table format reflects the nested general linear models experimental design (SAS 1988).

| CREEK | LOCATION | DEVELOP. STAGE | INCUBATION HABITAT | | | | BrYr Mean | | Creek Means |
| | | | Preferred | | Marginal | | | | |
			1993	1994	1993	1994	93	94	93/94
Bivouac	Upper	1	-	13.91	-	19.30			
		2	-	0.00	-	8.36			
		3	-	0.00	-	0.00	-	7	
	Lower	1	-	9.85	-	20.14			
		2	-	0.00	-	0.00			
		3	-	0.00	-	1.05	-	5	- / 6
Gluskie	Upper	1	70.65	34.39	74.48	56.14			
		2	64.46	8.49	63.09	55.46			
		3	35.06	5.26	62.92	-	61	32	
	Lower	1	21.55	13.95	60.64	20.20			
		2	26.06	-	59.78	-			
		3	21.95	-	49.52	-	40	17	51/28
Forfar	Upper	1	26.33	3.99	49.30	6.62			
		2	21.29	1.50	47.00	0.00			
		3	24.53	1.75	47.58	0.00	36	2	
	Lower	1	69.76	29.91	62.06	31.97			
		2	71.04	31.88	67.09	32.32			
		3	69.50	33.03	40.89	14.12	63	29	50/16
Kynock	Upper	1	69.59	61.45	61.33	64.71			
		2	67.44	63.74	55.34	59.42			
		3	69.99	59.80	54.91	60.02	63	62	
	Lower	1	34.40	64.09	22.84	60.44			
		2	34.16	60.20	21.03	58.61			
		3	36.26	57.36	21.76	51.76	28	59	46/60
		Mean	46	25	51	30	49	27	38

99

APPENDIX C

Watershed and Broodyear stream and incubation physical parameters

Appendix C1. Summary of stream and intragravel physical parameters by habitat classification and sample period for all study streams combined (n=4).

HABITAT	DATE	n	VELOCITY (m/s)	DEPTH (cm)	STREAM TEMPERATURE (c)	INTRAGRAVEL TEMPERATURE (C)*	STREAM DISSOLVED O2 (mg/l)*	INTERGRAVEL DISSOLVED O2 (mg/l)*	SURFACE SUBSTRATE COMPOSITION *	RELATIVE PERMEABILITY INDEX (ml/s)
MARGIN	Jul-93	31	0.51 (0.28)	26.5 (14.9)	8.3 (0.6)	8.4 (0.6)	10.2 (0.4)	9.6 (0.7)	3.8 (0.5)	39.5 (26.0)
	Sep-93	32	0.19 (0.18)	13.3 (8.7)	5.8 (1.0)	5.9 (1.1)	11.0 (0.5)	9.3 (2.5)	3.6 (0.7)	22.7 (18.2)
	Dec-93	6	0.23 (0.18)	15.8 (10.0)	0.2 (0.2)	0.2 (0.3)	12.4 (0.3)	11.7 (0.4)		
	Apr-94	28	0.28 (0.20)	24.5 (12.2)	1.9 (1.1)	1.8 (1.0)	12.4 (0.6)	10.6 (2.3)	3.4 (1.0)	23.6 (14.5)
	Jul-94	35	0.36 (0.24)	20.3 (12.0)	10.6 (1.0)	10.5 (0.9)	10.1 (0.3)	8.7 (1.9)	3.9 (0.9)	23.1 (16.4)
	Sep-94	36	0.15 (0.16)	13.3 (9.0)	7.8 (0.8)	8.0 (0.8)	10.7 (0.4)	8.7 (2.8)	3.3 (1.0)	18.6 (12.9)
	Dec-94	2			0.0 (0.0)	0.0 (0.1)	12.6 (0.1)	11.7 (0.3)		
	Mean	**168**	**0.28 (0.25)**	**19.0 (12.5)**	**6.7 (3.3)**	**6.8 (3.3)**	**10.9 (0.9)**	**9.4 (2.3)**	**3.6 (0.9)**	**25.3 (19.4)**
THALWAG	Jul-93	36	0.59 (0.30)	40.6 (16.3)	8.3 (0.5)	8.3 (0.4)	10.3 (0.4)	9.5 (1.2)	3.9 (0.5)	35.1 (24.1)
	Sep-93	28	0.32 (0.19)	17.3 (6.3)	6.1 (0.8)	6.2 (0.8)	10.9 (0.4)	9.5 (1.5)	3.8 (0.5)	26.1 (19.1)
	Dec-93	7	0.21 (0.14)	17.0 (8.9)	0.1 (0.2)	0.2 (0.2))	12.4 (0.3)	11.5 (0.9)		
	Apr-94	43	0.45 (0.22)	34.0 (12.9)	2.1 (1.1)	2.1 (1.0)	12.3 (0.5)	11.5 (0.9)	3.9 (0.5)	19.9 (11.7)
	Jul-94	40	0.42 (0.24)	26.1 (12.9)	10.9 (1.1)	10.8 (1.3)	10.0 (0.4)	8.0 (3.0)	4.3 (0.8)	23.6 (19.4)
	Sep-94	34	0.37 (0.19)	19.1 (9.8)	8.2 (1.0)	8.2 (1.0)	10.6 (0.4)	9.7 (1.1)	3.9 (0.7)	25.6 (21.7)
	Dec-94	3			0.0 (0.0)	0.0 (0.1)	12.7 (0.4)	12.2 (0.2)		
	Mean	**191**	**0.43 (0.24)**	**27.7 (14.9)**	**6.7 (3.5)**	**6.7 (3.5)**	**10.9 (1.0)**	**9.8 (2.1)**	**4.0 (0.6)**	**25.8 (19.9)**
POOL	Jul-93	8	0.32 (0.22)	47.4 (7.6)	8.7 (0.2)	8.7 (0.16)	9.9 (0.6)	9.3 (1.0)	3.3 (0.8)	19.0 (6.7)
	Sep-93	25	0.07 (0.05)	40.7 (22.6)	6.6 (1.9)	6.6 (1.8)	11.0 (0.4)	10.3 (0.8)	3.2 (0.5)	25.5 (11.6)
	Dec-93	18	0.11 (0.10)	48.4 (11.8)	0.0 (0.1)	0.0 (0.1)	12.3 (0.2)	11.6 (0.6)		
	Apr-94	7	0.16 (0.09)	50.4 (8.8)	1.9 (0.8)	1.9 (0.55)	12.3 (0.4)	9.70 (3.5)	2.3 (1.3)	20.8 (16.4)
	Jul-94	10	0.30 (0.12)	35.8 (21.5)	11.5 (1.2)	11.6 (1.3)	9.8 (0.4)	9.3 (0.5)	4.6 (0.3)	27.0 (35.1)
	Sep-94	23	0.12 (0.08)	37.7 (16.8)	8.2 (0.9)	8.3 (0.8)	10.6 (0.3)	8.4 (2.6)	3.3 (0.9)	27.0 (18.9)
	Dec-94	1			0	0.1	12.5	8.5		
	Mean	**92**	**0.14 (0.13)**	**42.2 (17.8)**	**6.0 (3.9)**	**6.0 (4.0)**	**11.1 (1.0)**	**9.8 (2.0)**	**3.4 (1.0)**	**25.0 (19.7)**
OFF-CHANNEL	Jul-93	17	0.13 (0.13)	39.8 (16.1)	8.3 (0.5)	8.1 (0.6)	9.9 (0.3)	6.0 (3.5)	2.9 (0.9)	29.7 (26.2)
	Sep-93	18	0.02 (0.04)	19.0 (18.8)	6.2 (0.6)	6.5 (0.6)	10.0 (1.5)	6.2 (3.3)	2.5 (1.0)	14.9 (11.5)
	Dec-93	15	0.04 (0.06)	17.5 (11.9)	0.1 (0.2)	0.4 (0.4)	10.1 (2.9)	8.1 (2.9)		
	Apr-94	18	0.12 (0.15)	27.5 (27.5)	2.3 (1.1)	2.1 (0.9)	12.0 (0.5)	7.6 (4.6)	2.8 (1.3)	21.3 (13.1)
	Jul-94	18	0.09 (0.08)	27.6 (16.8)	10.9 (1.2)	10.3 (1.1)	9.9 (0.4)	5.5 (3.6)	3.0 (1.2)	16.7 (9.4)
	Sep-94	11	0.05 (0.07)	18.5 (11.0)	8.1 (0.7)	8.2 (0.6)	10.0 (1.0)	5.5 (4.3)	3.1 (0.8)	17.6 (8.9)
	Dec-94	2			-0.1 (0.1)	-0.1 (0.1)	12.8 (0.4)	11.4 (0.6)		
	Mean	**99**	**0.08 (0.10)**	**25.5 (19.6)**	**5.8 (3.9)**	**5.7 (3.7)**	**10.4 (1.6)**	**6.6 (3.8)**	**2.8 (1.1)**	**19.9 (15.7)**

* NOTE:
Intergravel measurements taken at substrate depth of 20 cm
Surface Substrate classification:
1 = Silt, 2 = Sands, 3 = Pea Gravel, 4 = Gravel, 5 = Cobble, 6 = Boulder

Appendix C2. Stream and intragravel physical parameters for both broodyears (1993, 1994) combined over all locations, sites and seasons for the selected study streams (n=3) of the early Stuart sockeye stock.

| VARIABLE | CREEK | | | p < 0.05 |
	GLUSKIE	FORFAR	KYNOCK	
VELOCITY (m/s)	0.27	0.26	0.29	no
Std. Err.	0.02	0.02	0.02	
Range	0.00 - 1.45	0 - 1.23	0 - 1.38	
n	173	193	174	
DEPTH (cm)	26.4	25.7	29.3	no
Std. Err.	1.2	1.1	1.5	
Range	3.0 - 75.0	1.0 - 100.0	2.0 - 132.0	
n	173	193	174	
STREAM TEMP (C)	6.0	6.4	6.9	no
Std. Err.	0.3	0.2	0.3	
Range	-0.1 - 10.9	-0.2 - 10.8	-13	
n	171	196	181	
INTRAGRAVEL TEMPERATURE (C)	6.0	6.4	6.9	no
Std. Err.	0.26	0.24	0.29	
Range	-0.1 - 10.6	-0.1 - 11.0	-0.1 - 12.8	
n	171	195	182	
SURFACE SUBSTRATE	3.7	3.4	3.7	***
Std. Err.	0.1	0.1	0.1	
Range	1.0 - 5.2	1.0 - 5.0	1.0 - 5.0	
n	159	180	156	
Duncans	A	B	A	
STREAM DISOLVED OXYGEN (mg/l)	11.1	10.9	10.5	***
Std. Err.	0.1	0.1	0.1	
Range	8.2 - 13.3	7.6 - 13.1	3.6 - 12.5	
n	171	196	181	
Duncans	A	A	B	
INTRAGRAVEL DISOLVED OXYGEN (mg/l)	9.7	8.9	8.8	***
Std. Err.	0.2	0.2	0.2	
Range	0.3 - 12.9	0.3 - 12.4	0.2 - 12.1	
n	171	195	182	
Duncans	A	B	B	
PERMEABILITY (ml/s)	22.7	24.2	27.0	no
Std. Err.	1.3	1.5	1.8	
Range	3 - 84	0 - 120	5 - 129	
n	154	171	146	