

ACTIVITY AND BEHAVIOUR IN
SPAWNING SOCKEYE SALMON

by

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Technical Diploma, British Columbia Institute of Technology, 1989
B.Sc., Simon Fraser University, 1994

A THESIS SUBMITTED IN PARTIAL FULFILMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Forest Sciences)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
June 1999

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Date Aug 20/99

ABSTRACT

Total energy expenditures and muscle activity have been measured in spawning salmon but behaviour specific energy-use has never been measured directly. This research used electromyogram (EMG) telemetry, combined with behaviour observations to assess activity levels and estimate relative energy use during spawning in sockeye salmon, *Oncorhynchus nerka*. My main objectives were to: assess the ability of EMG transmitter technology to discriminate between the rate of muscle activity during short duration specific behaviours and general activity, and; use these data to compare the total activity between spawning stages, sex, and year.

EMG data were converted to rate of tail beats and, using synchronized clocks, were matched with specific spawning ground behaviours. Rate of tail beats, behaviour duration, and behaviour frequency were multiplied to estimate the total tail beats for the mean duration of male and female fish on the spawning grounds. Sequential reproductive stages were observed in the spawning stream. Males and females were given a 'status' designation corresponding to their reproductive stage. Behaviour specific analysis of total tail beats for each behaviour revealed that males and females of different reproductive status had different mean total tail beats for some behaviours. Total tail beats for males and females in two consecutive years revealed that females utilized more tail beats in one year and equal tail beats to the males in the other year. Total tail beats were strongly associated with duration of each fish in the spawning stream. This along

with other observations suggests that the majority of energy expended on the spawning ground was due to non-specific general behaviours such as "holding position" (eg. behaviours not involved in act of spawning or defense/competition for spawning areas). EMG technology appears to be a highly effective tool for studying spawning ground activities in salmon.

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ACKNOWLEDGEMENTS

I would like to thank my thesis committee - Dr. Scott Hinch, Dr. Michael Healey, and Dr. Kathy Martin for their valuable advice in the design and development of my thesis. To Dr. Scott Hinch I extend my gratitude and appreciation for his experience and support while I developed my thesis. I would like to thank Pier van Dishoeck, an excellent field technician, for his enthusiastic assistance in the field. The Department of Fisheries and Oceans assisted by allowing me to obtain sockeye salmon from the fish fence in Gluskie Creek and providing ancillary field data. My field research and thesis development was supported by the Fraser River Action Plan through Canada's Green Plan and an NSERC grant to Dr. Scott Hinch.

R.G.L.

In memory of Dr. Donald Guthrie

“Beyond is the great and wild sea
with its living things too many to number,
creatures both small and large.
Here move the ships,
and when come those great beasts,
you chase them for the sport of it.
All of them look to you
to give them their due season.
You give it to them; they gather;
you open your hands,
and they are filled with good things.
You show your face, and they are fearless;
you take away their breath,
and they return to ashes.
You send forth your Spirit, and they are renewed,
and you renew the face of the earth”.

- *Randal Lake*, adapted from *Psalm 104*.

INTRODUCTION

Pacific salmon stop feeding prior to initiation of their upstream spawning migration. Completion of the migration and successful spawning are dependent on energy reserves that the fish possess at the start of migration. Two studies have explored energetic costs of upstream migration in sockeye salmon (Idler and Clemens 1959, Gilhousen 1980). This limits analysis to quantifying the total energy used during stages of Pacific salmon migration but not behaviour-specific analysis of energy expenditure associated with spawning. Although qualitative descriptions of the behaviour of Pacific salmon, *Oncorhynchus*, on the spawning grounds have been made, measures of spawning ground energy expenditure are rare. Spawning studies could not look in detail when and where these costs were incurred.

Recent developments in radio transmitter technology allows the quantification of muscle contractions. Hinch et al. (1996), Hinch and Rand (1998), Rand and Hinch (1998) used Electromyogram (EMG) radio transmitters to study the behaviour and lateral swim muscle activity during upstream migration of the early Stuart sockeye salmon through specific reaches and areas of difficult passage in the Fraser River. Laboratory and field models of muscle activity were developed. Results of these studies show that EMG radio telemetry is successful in identifying reaches and features of difficult passage, and provides insight into the behaviour and muscle activity of fish during upstream migrations.

The field activity of lake trout (*Salvelinus namaycush*) during their reproductive period in White Pine Lake, Ontario, was used to infer spawning activity of lake trout (Weatherley et al. 1996). The EMGs were characteristic of similar EMGs obtained from spawning lake trout in a laboratory study (Kaseloo et al. 1996). This laboratory study was used to calibrate EMGs to activity for assessment of activity in the field, and led to the successful identification of spawning activity in at least one of two lake trout implanted with EMG transmitters in the field study done by Weatherley et al. (1996).

Although activity measures are not measures of potential energy, energy is defined as the capacity to do work (Betts 1976), and tail beats do work. Therefore, there is a relationship between activity (tail beats) and energy. Standardizing lateral swim muscle contractions for all activities as tail beats, allows comparison of 'tail beats' between different behaviour factors. Although the actual rate of energy expenditure is not yet known for this experimental approach, it is assumed that a standardized measure of work done (rate of muscle contractions regressed to rate of tail beats in a lab analysis) can be used as an index of activity among behaviour factors and may be associated with rates of energy expenditures. This requires an assumption that energy expenditure and activity are positively correlated, and that the rate of energy expenditure is the same at specific rates and duration of activity. Body constituent analysis if done frequently during stages on the spawning grounds, or measures of oxygen consumption in an appropriate laboratory study, may eventually allow the

development of an accurate model to convert different rates of muscle activity to actual energy expenditure in spawning sockeye salmon.

The general objective of this thesis is to measure muscle activity and standardize it as rate of tail beats (TB s^{-1}) and total tail beats (TTB). The following are specific objectives: 1) I will assess the ability of EMG technology to discern the muscle activity for very short duration behaviours. Specific behaviours, which are typically of short duration, will be correlated to EMG values to show if muscle activity can be quantified for these short duration behaviours. 2) Muscle activity will be compared between specific behaviors and general activity, and also among sexes, spawning stage, and spawning years. This will show how activity is used by different fish throughout their duration on the spawning ground. 3) This information will be used as a relative index of energy expenditure, to assess if the Fraser River sockeye salmon 'body constituent' conclusions of Gilhousen (1980), that energy expenditures are greater in males and consistent among years, are reasonable.

Gilhousen (1980) did not state assumptions that were used to calculate energy utilized by kilogram/fish or kilogram/fish/day. Back calculations revealed two possible unstated assumptions. It was found that Gilhousen used the same spawning ground duration between sexes in all years, and sometimes between years. A more precise evaluation of activity and life duration on the spawning grounds may provide greater understanding of sockeye salmon spawning activity.

BACKGROUND

Life History and Reproductive Behaviour of Fish.

Fish may partially or fully stop feeding during reproduction. Fasting may be adaptive when an absence or variability in food resources occurs. Energy utilized while searching for prey when it is scarce or absent, especially in an environment where there are many other spawning fish to compete with, may not be offset by energy obtained from captured prey. In a food abundant environment fasting may prevent spawning fish from eating their own embryos. Reproductive success depends on utilization and re-allocation of stored somatic energy and effective behaviour tactics to support reproductive effort. Reproductive effort includes energetic costs of migration, mating, spawning, parental care, and costs to future reproduction (Clutton-Brock 1984). This section will examine reproductive effort and associated costs to fish.

Fish have various life history strategies which ultimately are adaptations to optimize reproductive success. Reproductive success may be defined as the number of offspring surviving to reproductive maturity relative to those produced by other fish in the population (Wootton 1985). Reproductive effort can be defined as the accumulated investments, or costs, during a single reproductive event. Examples of reproductive effort include: migration, gamete development, spawning behaviours, and parental care (Roff 1992). Reproductive effort has two types of associated costs. These are: the energy utilized during reproduction,

and costs to future reproduction and survival (Clutton-Brock 1984; Roff 1992). When surplus somatic energy is insufficient for reallocation to reproduction, future growth, fecundity, and survival may be reduced.

Salmonids are a diverse family of fishes including both semelparous (Pacific salmon) and iteroparous species. The life history and evolution of salmonid species are among the most studied. However, life history studies rarely quantify behaviours and none have quantified specific behaviours energetically. The life history of Pacific salmon species are similar in a general sense, and sockeye salmon are typical of the other species (Burgner, 1991).

Most sockeye salmon juveniles rear in lakes for 1 or 2 years, therefore spawning streams have close access to lakes. However, some juveniles may rear in rivers or their backwater pools. A few stocks are prevented by river flows from migrating upstream to lake rearing habitat and migrate downstream to the river estuary instead. For example, in British Columbia, emergent fry in the Harrison River tributary in the lower Fraser River migrate out to the Fraser River estuary. Alternately, some sockeye salmon stocks, such as the Cultus Lake stock beach spawn in the rearing lake itself. Upper Fraser River stocks are typical of sockeye salmon in that fry emerge from streams and migrate upstream or downstream, in the appropriate direction, to lake rearing habitat. Sockeye salmon are distinctive from other Pacific salmon species in their predominant requirement for lake rearing habitat with associated spawning streams (Burgner 1991).

Sockeye salmon juveniles smolt and migrate down to coastal ocean waters in the spring. British Columbia stocks of southern origin migrate northward along the coast of British Columbia and Alaska while feeding in the nutrient rich waters of the continental shelf. Juveniles move offshore into the deep Alaskan gyre sometime during late fall or winter. Depending on the stock and individual they circulate in the gyre from one to four years, while developing into sub-adults (Burgner 1991).

Food abundance is often patchily distributed and variable between years. Growth rate effects survival because predation on sub-adults is size dependent (Stearns 1976). Swim speed is correlated with fish length and lateral swim muscle mass. Burst swimming away from predators is an important method of escape in the open ocean. It retains its importance during upstream spawning migrations through high velocity obstacles in rivers.

As two to five year old maturing adults, British Columbia sockeye salmon exit the Alaskan gyre into coastal waters. Southward migration follows the coast using homing cues until the river estuary is reached. Schooling in the estuary is common and the duration is greater with later arriving stocks. Feeding may stop weeks prior to fresh water entry (Foerster 1968). Time of schooling, fresh water entry, migration distance, and time to the spawning ground varies between stocks. The 'upper river' early Stuart River sockeye salmon enter the Fraser River from the ocean in July and migrate 1200 kilometers. In contrast, the 'lower

river' Cultus Lake stock enters the Fraser River from the ocean in September and has a short migration of 88 kilometers (Gilhousen 1960).

Upstream migration of sockeye salmon typically consists of mixed stocks for most of the multi-stock systems. Fraser River stocks have exceptionally discrete peaks of migrations such that peak migration timing allows identification of the different stocks while still in the Fraser River mainstem (Gilhousen 1960; Killick 1955). These discrete migration peaks are an adaptive effect of the extremely different environmental conditions existing in each stocks' migration route and spawning location. Average egg incubation temperature is often different between spawning locations and effects the rate of egg development. Timing of spawning and subsequent fry emergence is critical for fry survival (Brannon 1987).

Temperature and flow conditions encountered by adult sockeye salmon vary between migration routes and years, effecting energy utilization, migration behaviour, and survival (Idler and Clemens 1959; Gilhousen 1980; Rand and Hinch 1998; Hinch and Rand 1998). Many large rivers have mean velocities which exceed the maximum sustained swim speed of sockeye salmon (Osborne 1961; Brett 1965). Hinch and Rand (1998) studied the relationship of local environment and fish characteristics to swim speeds and energy use in adult sockeye salmon. They used identical electromyogram telemetry on the same years and stock of early Stuart sockeye salmon as I used in this thesis. They demonstrated that upriver migrating fish selected low velocity pathways and

reverse flow pathways (i.e. eddies). Fastest migration speeds (m s^{-1}) were through low velocity reaches and slowest through constricted reaches such as Hells' Gate canyon, considered the most difficult passage point in the river. Only differences in reaches significantly accounted for differences in migration speed. Differences in swim speeds (tailbeats s^{-1}) and energy use between years appeared most correlated with river flow dynamics.

When reaching the spawning grounds some stocks may school for a variable time before beginning to spawn. Lower river stocks may school for weeks. Their fresh water residence is almost as lengthy as upriver migrating stocks. Early river entry and holding is variable in sockeye salmon stocks and other Pacific salmon species.

Most salmonids spawn in streams. The behaviour of lake spawning populations is rarely observed and studied, so it will not be further discussed. Stream spawning behaviour of Pacific salmon species is highly similar, but differences exist with respect to some male spawning tactics. No single study appears to encompass the full compliment of behaviour in sockeye salmon, or other salmon species. Often, contests and territory defense behaviours are lumped together as 'aggressive acts' (McCart 1971). A general review of studies is required to describe the behaviour of spawning salmon.

Riffles are preferred sites for establishment of spawning territory and redds. Hoopes (1972) found streambed morphology was the single most important factor in selection of a spawning territory, or redd. Gravel-cobble

substrate found in riffles is preferred. Higher gradient sites with cobble bottoms are used less often, and low gradient pools are used least. The tail-spill is used most often in pools, and it should be noted that water accelerates out of the pool at these sites. In riffles, females chose gently sloping sites where the excavated tail-spill created while nest digging provided a slight rise. Spawning occurred almost always in riffle gradients between 0.5% to 2.0%. Sockeye salmon spawning in Four Mile creek, tributary to Babine Lake, had a mean water flow over the nests of $21.9 \text{ cm}\cdot\text{s}^{-1}$ (McCart 1971). Establishing territory for spawning may occur by selection of an unoccupied site, or displacement of another fish by aggression. When a male or female is seeking a spawning territory, they may instead join a territory held by a fish of the other sex. Spawning territory is usually established by the female and subsequently joined by a male (Hanson and Smith 1967).

Hanson and Smith (1967) studied mate selection in sockeye salmon and found that males prefer to mate with a larger female, possibly due to her vigor and fecundity. Large males usually defeat smaller males during contests for females. Therefore, the largest males mate with the largest females and the smaller males mate with the smaller females. This has the effect of mated males being the same size or slightly larger than their female. When the males greatly outnumber the spawning females, the largest males will mate with females of all sizes. Smaller and senescing males may associate with spawning pairs as subdominant satellites. Size was shown to be an important determinant in male

dominance in sea trout which may have up to 10 males in association with a spawning female (Evans 1994).

Behaviour interactions between a male and female are occasionally called 'courtship' behaviours (ex. quivering), but I have not seen any study that provides evidence that these are courtship behaviours (i.e. no studies have defined and identified courtship behaviour in sockeye salmon). Size assortive mating does occur, but by dominance contests between males for possession of a territory and access to a female. Females may chase away smaller males and accept equal size or larger males. Female sockeye salmon spawning with larger males appear to extrude all their eggs in less time than other females (Foote 1989). Mate choice by males and females may be by morphological characteristics, with body size being strongly assessed by a potential mate.

Younger jack males occur in spawning sockeye salmon populations. They are older and larger than the jacks associated with coho salmon populations, and have some development of secondary sexual characteristics including a bright red or pink color. Because of their larger size and lack of crypsis, they may use a satellite strategy, spawn in extremely marginal spawning habitat, or spawn with female kokanee (the non anadromous form of sockeye salmon) (Foote and Larkin 1988). Male kokanee often spawn as satellites with anadromous sockeye salmon.

Pacific salmon usually dig a series of 3 to 5 successive nests known as a redd (Foote 1989). One nest precedes another in an upstream direction. Tautz and Groot (1975) reported chum salmon, *O. keta*, and rainbow trout, *O. mykiss*,

spawning in a flume started digging at sites with an upwelling flow. The upwelling could be created by placing a rise of stones or wood on the bottom. The female would drift backwards until its tail encountered the acceleration of the upwelling flow. Digging would commence immediately upstream. When chum salmon females were offered a site with upwelling but no substrate, and a site with gravel substrate but no upwelling, digging occurred in the site with upwelling and no substrate. Sites with substrate and upwelling were preferred most. Rainbow trout initiated digging at sites of upwelling. Heard (1972) observed the spawning behaviour of pink salmon in a tank with varied flow rates. During low flows (0.9 L s^{-1}) the fish milled about the tank or held at the side of the tank, and completely ignored previously established redds. The flow was generally similar to a pool. During higher flows (7.65 L s^{-1}), with a velocity 'upstream' of the redd of about 15 cm/s , females moved back onto their redd and defended it from other females. Female digging commenced and males appeared more active. It should be noted from the synthesis of information that the female appears to be oriented to the point of commencement of digging by an acceleration of water flow. Each subsequent excavation creates an upwelling and acceleration of water flow. Given a serial pattern of excavating and backfilling nests, the direction of redd digging would always proceed in an orderly upstream direction.

McCart (1969) studied the nest digging behaviour of sockeye salmon in tributary streams of Babine Lake, British Columbia. The females constructed the

nest by repeated digging over the same area. A 'dig' consisted of a continuous series of body flexures while in a horizontal position. Between digs the female was positioned immediately below the nest excavation. Occasional probing of the nest occurred by the female settling into the nest with pectoral, pelvic, and anal fin extended. The frequency of this activity increases as gamete release approaches. A dig begins with the female moving upstream over the nest and turning on her side with pectoral and pelvic fins extended. A rapid series of body flexures occurs, dislodging substrate with the caudal peduncle and fin. The dislodged substrate drifts and resettles slightly downstream of the dig site. Successive flexures often carries the female forward and upward. After the dig, the female returns to a position downstream of the nest.

The frequency of digging changes before and after a gamete release (Belding 1934; White 1942; Briggs 1953; Sheridan 1960; Mathisen 1962; McCart 1969; Tautz and Groot 1975). Tautz and Groot (1975) recorded diel periodicity of chum salmon digging, and noted an abrupt increase associated with gamete release. Sheridan (1960) studied the frequency of digging of female pink salmon before and after gamete release, in two streams in south-east Alaska. One observation was made in each stream. In both events the females dug at a regular rate of about 1 dig min.⁻¹ prior to gamete release. As gamete release approached, digging slowed or stopped and the female increased probing. Immediately after gamete release each female dug at 7 and 9 digs min.⁻¹. As the nest became backfilled, the digging slowed to frequencies similar to before gamete release.

This also coincides with the backfilling of the nest becoming the excavation of the next nest. Increased digging after gamete release was reported for sockeye salmon (Mathisen 1962), Atlantic salmon, *Salmo salar*, (Belding 1934), and for coho salmon, *O. kisutch*, (Briggs 1953).

McCart (1969) reported the duration, number of flexures per dig, and frequencies of digs. Dig frequency was about 1-min.^{-1} before gamete release and about 5.4-min.^{-1} after gamete release. The number of flexures and duration per dig was inversely related to the frequency of digs. Flexures decreased invariably to 2 per dig after gamete release. An increase in digs and decrease in flexures after gamete release is suggested as a quicker but more careful covering of eggs to prevent predation or dislodgment of eggs downstream. The force of the final flexure is used to turn the body, facilitating a rapid return to the bottom of the nest. It is suggested this is adapted to increase the speed with which the female can begin the next dig. Males also dig but do not appear to contribute to preparing the nest. Substrate was rarely lifted and was not always oriented to the nest. Male digging appeared to occur after intruders swam past the males' territory, after aggressive interactions, in response to aggression, in response to incomplete spawning acts, and often without any interactions. McCart (1971) suggests this is adapted as an alternative to aggression and therefore fits the definition of a displacement activity as defined by Tinbergen (1952).

Between digging a nest and backfilling it, a female and male(s) must synchronize a gamete release for optimal fertilization of eggs. As a spawning

female develops a redd, the male regularly quivers the female. The male positions himself downstream to the side of the female and near her body. Quivering appears to the observer as a short duration, high frequency vibration of the males' body. This behaviour is reported to provide a stimulus to the female which provides feedback to the male indicating the females' reproductive state (Satou et al. 1991).

As the nest becomes more developed, female digging slows and probing the nest occurs more often (Needham and Taft 1934; Sheridan 1960; McCart 1971). This often stimulates the male(s) to approach the nest. The female will often follow the probe with a dig. As female egg release approaches, she appears to be probing in the bottom of the nest but digging does not occur. One or more males rush in and jostle for position. If the female does not release eggs the males leave the nest. This behaviour may occur repeatedly until the female releases eggs. The female gapes her mouth open and vibrates convulsively. Eggs are expelled from the vent and within seconds, the male(s) expel milt from their vents. This is visible to the observer as a white 'puff' or plume drifting out of the nest. Sometimes when the female does not expel eggs, males may still expel milt, creating a false spawn. The repeated probing or 'crouching' in the bottom of the nest immediately before egg release may ensure male attendance and synchrony of egg and sperm release. The female may use the stimulus of males rushing into the nest to assure fertilization will occur when she expels eggs.

Males dominant on a redd territory with a female have the best advantage for fertilization of eggs due to proximity (Chebanov et al. 1983). Other males may rush in and jostle for position near the female, which correlates with greater fertilization success for the male. Subdominant satellites, jacks, male kokanee, and other dominants have all been observed to participate in the rush to fertilize eggs. The occurrence and magnitude of multiple male morphologies and associated reproductive tactics varies between species, populations, and years. This suggests both genetic and environmental factors effect the success and frequency of the various male tactics for achieving fertilizations of eggs.

After the gamete release, males immediately disperse in the stream (Greeley 1932; Burgner 1991). They may be exploring other fertilization opportunities. A dominant male salmon may hold to one side of its territory and may not contest intrusions by other males for a period of time (Keenleyside and Dupuis 1988). Dominant coho salmon males have been reported to leave and join another female in the males' territory (Prince 1977).

Females begin rapid nest backfilling typified by the frequent short duration digs which occur after gamete release. Once the female has extruded and buried her eggs the dominant male will usually leave and seek other fertilization opportunities. The female remains to guard the finished redd until death. She will defend the redd territory against intrusions by females and all males, regardless of dominance (McCart 1971).

Contests occur between spawning salmon to defend or take over redd territories. Territories include substrate for nesting, an attending dominant male for females, and primary access to a spawning female and opportunities for fertilizations in adjacent redds for dominant males. Two categories of contesting behaviours exist: displays, which involve no physical contact but may initiate flight or fight responses in other fish, and, physical aggression, which involve physical contact with another fish.

Lateral displays are the raising of the dorsal fin to another fish, or raising the dorsal fin combined with a paired lateral upstream swim between two males. I will clarify these two behaviours for my study fish, and suggest two separate descriptions that accurately define the meaning of 'lateral'. Females may raise their dorsal fin, but have not been reported engaging in lateral upstream swims.

Contest behaviours occur throughout spawning. Males contest to gain and retain access to egg fertilization opportunities. Females contest to gain and retain access to spawning substrate, and continue after spawning to guard the completed redd with its fertilized eggs against disturbance by other fish. From the general review of salmon behaviour in this chapter, one conclusion can be made. Male and female salmon behaviours are adaptations to optimize fertilization and development of eggs, and thereby reproduce successfully (Stearns, 1976).

All species partition energy into reproduction or growth depending on their reproductive strategy, life history stage, and ecological circumstances (Roff

1992). When sockeye salmon begin spawning, they have partitioned stored somatic energy into reproductive growth. Remaining somatic energy is not replenished due to the absence of feeding. All reproductive behaviours including the completion of gamete releases must be done with remaining somatic energy. Therefore, the amount of energy utilized during specific spawning behaviours may effect spawning behaviours used.

Spawning Behaviour, Activity, and Energetics in Fish.

Fasting mature salmon have often been used for energetic expenditure studies because feeding (energy intake), the main confounding variable is absent. Somatic proteins and lipids are metabolized during upstream migration. The earliest known study of fish bioenergetics was by chemical analysis of the changes in muscle and gonads of female Atlantic salmon reproductively maturing in the Rhine River (Miescher-Rusch 1880). This seminal study recognized the role of energy intake and allocation to maintenance metabolism, growth, and reproduction including the energy re-allocation from somatic tissue to gonads in fasting mature salmon. Since then, fish bioenergetics has been studied by various methods including: 1) 'direct calorimetry' in which heat production is measured in a calorimeter chamber, 2) 'indirect calorimetry' in which oxygen consumption is measured, and 3) 'body composition changes' measured by bomb calorimetry or chemical analysis of serial samples of body tissues from a fasting population (Brett 1973). Many of the early fish energetics studies were done by R. Brett and primarily on salmonids.

Brett (1965) used a tunnel respirometer to measure oxygen consumption of juvenile and sub-adult sockeye salmon at standard (resting) and active (maximum oxygen uptake) metabolism. With large fish, tail-beat frequency was correlated with oxygen consumption rates. Maximum 60 minute sustained swim speeds were higher as fish size increased; however, when the swim speeds of all fish were expressed in body lengths s^{-1} a decrease in relative swim speed was indicated for

larger fish. Despite an increase in body musculature and metabolic scope accompanying increased size, increased hydrodynamic drag is only partially compensated by increased size. Metabolic processes do not keep pace with the increasing energetic cost of higher sustained swim speed for larger fish.

In a later study, Brett (1973) examined the relationship of weight, length, and temperature to swim speed and metabolic rate. Relative swim speed was reduced in larger and longer fish. Optimal sustainable swim speeds for all sizes of fish was attained at about 15°C. Metabolic rate increased with temperature up to 15°C, which correlated with the optimal sustained rate for swim speed. Fish weight had least effect on active metabolic rate at temperatures below 10°C. Fish weight had about equal effect on standard metabolism at all temperatures (5-20°C).

Brett (1973) used a flume to exercise juvenile and maturing adult sockeye salmon for long periods of sustained swimming (10-20 days). At the end of the trial, the fish were sacrificed and frozen for proximate analysis and calorimetry. Similarly, fish were also exercised for the same period in a respirometer with identical flow rate. Oxygen consumption rates in relation to the performance by the fish in the respirometer was measured. Water, protein, fat, and carbohydrate constituents of the flume exercised fish were determined. Calorimetry from the same sample population was determined either with a bomb calorimeter or calculated from proximate analysis using known caloric equivalencies for the constituents. Subsequent analysis of data showed caloric loss from body

constituents exceeded estimates from oxygen uptake by an average of 19.8%. Excretion of partially metabolized constituents from the vent and gills is suggested as the source of difference from the estimate. These partially metabolized products may be byproducts of anaerobic activity. Anaerobic activity could occur during the exercise regime or periodic bursts of activity, such as aggressive interactions between fish.

Idler and Clemens (1959) did one of the first comprehensive studies on energy utilization by spawning salmon. Gilhousen (1980) did a detailed re-evaluation of Idler and Clemens (1959) data. Using serial analysis of separate body constituents, they examined energy partitioning to gonads and locomotion during river migration and spawning in sockeye salmon. The sampling years were between 1956 to 1958 with some years not sampled for some stocks. They examined three upper river stocks and three lower river stocks from fresh water entry to their spawning grounds. The upper river stocks had correlated longer migration times, shorter schooling times on arrival at the spawning grounds, and greater energy expenditure and re-allocation to gonads during migration. Lower river stocks underwent maturation while schooling for weeks near their spawning grounds. Analysis was also done upon arrival at the spawning grounds and again at death for the early Stuart sockeye salmon in 1956, 1957, and 1958.

During the upstream migration and in the spawning stream somatic energy is depleted. Gilhousen (1980) reported that fat provided more than 70% of the migration and spawning energy in the upper Fraser River sockeye salmon.

Muscle protein was increasingly utilized later in the migration and spawning. Re-allocation of stored soma to gonads during migration was also recognized. A portion of utilized protein was replaced with water, reducing loss of mass and increasing relative gravity. Muscle protein was reduced and the trimmings gained weight during migration in males, apparently for secondary sexual development. In females, an equal amount of muscle protein appeared to be re-allocated to ovaries which gained weight and developed during migration. Testes were nearly fully developed early in migration.

Gilhousen (1980) also reported on energetics of spawning activity. The samples of the early Stuart sockeye salmon on their spawning grounds provided analysis of energy use by males and females for spawning ground activity. Samples were taken from fish entering the spawning stream and fish recently dead. Males are reported to have greater absolute and daily energy expenditure than females in both years.

Early Stuart sockeye salmon females re-allocate more somatic fat to gonad development during migration than males (Gilhousen 1980). In addition, males arrived at the spawning stream with more somatic fat than females, and dead males had more somatic fat than dead females. Jonsson et al. (1991) did a serial constituent analysis of migrating and spawning Atlantic salmon in south-western Norway. During spawning the utilization of somatic fat was greater in males than females, similar to sockeye salmon. Unlike sockeye salmon, spent female Atlantic salmon retained more somatic fat than males. This suggests the iteroparous

Atlantic salmon females utilize less somatic fat and/or re-allocate less somatic fat into gonad development than the semelparous sockeye salmon females.

Fishery scientists have long sought a means of accurate assessment of the amount and nature of locomotor activity in free ranging fish. Such information would permit precise estimates of the metabolic costs of daily activity and specific behaviours of a fish. This would serve as a useful tool for the evaluation of numerous ecological problems, including feeding, migrating, and spawning (Rogers et al. 1984).

Other methods besides body constituent analysis have been used to determine relative energy expenditure in fish. Activity, an index of energy use, has been measured using cameras, and remote sonic and radio telemetry. Cameras record physical activity such as tailbeats or pectoral fin sculling. Events can be visually measured by counts, duration, and degree of flexion of body or fins. Activity can then be correlated with calorimetric methods. For example, tailbeats s^{-1} has been converted to known oxygen consumption rates for a range of tailbeats s^{-1} (Brett 1973) and then to calorimetric equivalents.

Video cameras have been used to estimate field energetics. Krohn and Boisclair (1994) used a video method to record spontaneous activity in free swimming brook char, *Salvelinus fontinalis*, while simultaneously measuring oxygen consumption. Metabolic costs of spontaneous activity were estimated by combining these measures. Energy expenditure, measured by respirometry, during spontaneous swimming was, on average, six times higher than forced

swimming at constant speed and direction for juveniles weighing 5 - 11 grams. Fish may develop a more efficient swimming behaviour during forced swimming, and spontaneous swimming involves acceleration which may incur greater short duration metabolic costs. Metabolic costs of turning and accelerating may be an important component of activity energy expenditure in large fish (Webb 1995). This has implications for the study of spawning Pacific salmon, which turn and accelerate frequently during reproductive behaviour. Activity metabolism on sockeye salmon spawning grounds was found to equal and in some cases exceed river migration by 14% for females and 59% for males (Gilhousen 1980).

Hinch and Collins (1991) used video observations of free ranging male smallmouth bass, *Micropterus dolomieu*, defending nests during oviposition and until swim up larvae appear. Two nests, each guarded by a male and located within 15 m of each other, were continuously monitored using time lapse video and infra-red light for illumination. Guarding males were found to be active day and night, sculling pectoral and caudal fins constantly over the nest. Caudal fin beat rates were used to relate the costs of guarding swimming to non-guarding swimming. Using a respiration model for largemouth bass, *M. salmoides*, they estimated the energetic expenditure of nest guarding small mouth bass to be up to 60% higher than non-guarding. Predation of offspring was low for the nest guarding male, even though the male left the nest briefly. In an abandoned nest, predators took about 1 day to discover the offspring and another day before they were completely consumed. The male that abandoned this nest may have been

under energetic constraints. It did not feed during 11 days of observation, whereas the male that remained in the nest was observed to feed at a rate averaged 1 - 2% of its wet body weight per day. Energetic constraints of 24 hour per day nest guarding, continuous in-place swimming, reduced food intake, and brood defense may greatly reduce reproductive success in smallmouth bass.

Besides video observations, telemetry has also been used to estimate energetic costs in wild spawning fish. Remote sonic and radio telemetry requires a transmitter that measures biophysical and/or environmental parameters, then transmits them to a remote receiver. The receiver logs the data and can be downloaded into a computer. Transmitters are diverse in their capabilities. For example, accelerometers have been used to measure tailbeat frequency and amplitude, electrocardiogram (ECG) sensors to measure heart rate, and electromyogram (EMG) sensors to measure muscle contraction rate.

The advent of underwater biotelemetry since the 1960s has made it possible to track the movements of fish by simple location transmitters (radio or ultrasonic) attached to the fish. However, using this information to evaluate the metabolic costs of activity is difficult given the intricacies of fish behaviour and environmental conditions (Priede and Young 1977; Weatherley 1976; Weatherley et al. 1982). Progress in other aspects of underwater biotelemetry has led to the monitoring of physical and physiological variables such as tailbeat frequency (Stasko and Pincock 1976; Ross et al. 1981), swimming speed (Vogeli and Pincock 1980) and heart rate (Priede and Young 1977) in free ranging fish.

Attempts to deduce the metabolic costs of activity from data on these variables have also proved error prone (Rogers et al. 1981; Weatherly et al. 1982).

The technique of ultrasonic tagging was first used successfully by Trefethen (1956), and Johnson (1960) to track the movements of migrating salmon. Larger superficial transmitters were used by Poddubnyi et al. (1966) to observe the migratory movements of sturgeon, *Acipenser baeri*, in the River Volga. Henderson et al. (1966) and Hasler et al. (1969, 1970) used small stomach transmitters to investigate detailed orientation movements in freshwater fish. A similar technique was used by Yuen (1970) to track the movements of skipjack tuna, *Katsuwonus pelanus*. In general the transmitters used in these experiments were large, with the exception of Hasler et al. (1970), so only large fish could be used. Tracking was done by following the fish in motor boats fitted with hydrophones and receivers (Young et al. 1971).

Young et al. (1972) developed an ultrasonic tracking system to monitor the activity levels of small fish (> 200 grams) in their natural environment. Activity measurement units were designed to conform to units used in laboratory studies to approximate the metabolic cost of locomotion in fish (Brett 1964), so that it would be possible to estimate the relative importance of activity in free ranging fish. Sonic transmitters were attached externally to the lateral surface of the fish, below the dorsal fin. Four brown trout, *Salmo trutta*, with transmitters were released into Airthrey Loch, Scotland and tracked for 24 hour periods (Young et al. 1971). Swim speeds, fish locations, and activity levels were determined for 24

hour periods. Two fish were caught by anglers and were reported to have fought vigorously and one caught fish had insects in its stomach suggesting that fish had behaved normally after transmitter attachment and release.

There have been attempts to use heart rates of fish as indices of swimming activity, using ultrasonic methods (Kanwisher et al. 1974; Wardle and Kanwisher 1974; Priede and Young 1977) and radio telemetry (Frank 1968; Nomura and Ibaraki 1969; Nomura et al. 1972; Weintraub and Mackay 1975). Priede and Young (1977) have correlated trout heart rates with oxygen consumption in laboratory forced swims; therefore heart rate might be usable in an index of activity energetics. But heart rate in fish responds readily to environmental factors (Randall 1970), and because of this, and also because heart output is related to stroke volume, heart rate may not be a reliable index of physical activity or oxygen consumption (Weatherley et al 1980). For a further review of physiological telemetry studies, including heart rate telemetry, see Lucas et al. (1993).

Oxygen demands of muscular activity in fish at any given temperature are determined by biochemical processes at the tissue level (Weatherley et al. 1982). At the level of the whole muscle, strength, frequency, duration of contraction, and the bulk of the active muscle, will combine to determine its oxygen consumption. In most fish, the axial muscles, which are the main swimming muscles, consist of myomeres arranged in a bilaterally symmetrical series. Myomeres comprise most of the total bulk of the body muscle and are involved in

most body movements. For many species of fish, the demand for oxygen associated with the bodily muscular activity of steady state swimming can be explored by having a fish swim against a water current at constant velocity in a swim tunnel (Fry 1971).

However, in addition to its respiratory requirements, a contracting muscle generates a characteristic bio-electrical signal, the EMG, the configuration of which is related to the strength and duration of the muscle contraction. In the case of the fish myomere, which is one of a linear series, the EMG of any one myomere might be assumed to be representative of other myomeres. The configuration of the EMG of a representative myomere might be assumed to be highly correlated with oxygen consumption resulting from the activity of the entire myomere series (Weatherley et al. 1982).

Uematsu et al. (1979) described EMG recordings from spawning female chum salmon in a laboratory flume. Bipolar electrodes were implanted in both dorsal and ventral axial muscles. The electrodes were attached to an amplifier at the other end and displayed on an oscilloscope and photographed. Two spawning events were recorded and showed both dorsal and ventral axial muscles contracted convulsively during oviposition. All muscles where the electrodes were implanted fired simultaneously and corresponded with the time of egg discharge.

Rogers et al. (1981) and Weatherley et al. (1982) described a laboratory based radio telemetry system for the 'remote' detection of EMGs from the main

swimming muscles of rainbow trout. EMGs correlated well with activity and oxygen consumption rates under routine and constant swimming conditions. The system previously developed for field use (Rogers et al. 1984) had major problems associated with it. Transmitter functioning was too short, malfunctions occurred, externally attaching transmitters often resulted in dislodgment, and additional drag was imposed by the transmitter. An additional problem was that the EMG signal was difficult to store and process with computers into mean values of μV . These problems have recently been addressed (Kaseloo et al. 1991). Signal transmission of up to 7 months has been obtained using a radio transmitter packaged in laboratory fish. Problems with drag have been eliminated with internal implantation. Changes in transmitter design and packaging has greatly reduced transmitter malfunctioning.

Kaseloo et al. (1991) reported recent improvements of EMG telemetry. The technique employed in the past used radio telemetry transmitters to transmit EMGs from fish in the laboratory (Weatherley et al. 1982) or an ultrasonic version to do the same for free ranging fish (Rogers et al. 1984). The EMGs were detected by sensing electrodes implanted in the fish axial muscles. The EMG values could be used directly as indicators of the intensity of fish activity. Also, they could be calibrated to fish oxygen consumption measured over the same times in swims of selected velocities and duration, or over periods of spontaneous activity (Weatherley et al. 1982). The latter procedure gives, in

principle, the possibility of obtaining quantitative estimates of the metabolic costs of activity by free ranging fish.

McKinley and Power (1992) studied the activity and oxygen consumption of free ranging adult lake sturgeon, *Acipenser fulvescens*, using EMG radio telemetry. EMGs from the axial muscles were successful in long term monitoring of locomotor activity in the field, and subsequent estimates of correlated energy utilization. Demers et al. (1996) used EMG radio telemetry to determine the activity patterns of largemouth and smallmouth bass. Two largemouth bass and two smallmouth bass were captured in Ranger Lake, Ontario, and surgically implanted with EMG transmitters by the method of Kaseloo et al. (1992). The bass were released back into the lake with a shore based Yagi antenna to collect EMG signals for the whole lake. EMGs were collected for a period of months and allowed monitoring of daily activity levels for each fish. The fish were most active during the day, and tracking the movement of each fish allowed matching of distance traveled to activity level. All fish survived beyond the study period. After recapture, the incision site was completely healed and sutures were absorbed. No internal damage was noticed and the transmitters were encapsulated in connective tissue.

Kaseloo et al. (1996) used EMG radio telemetry in a laboratory study of the activity of spawning lake trout. One male and one female were surgically implanted with EMG transmitters and allowed to spawn in an artificial laboratory spawning flume. EMG values were successfully calibrated to spawning activity.

Weatherley et al. (1996) used the laboratory EMG values calibrated to activity values to monitor the spawning activity of free ranging lake trout. They were successful in determining one fish engaged in similar activity patterns as the laboratory fish, during the spawning period and at a known spawning location. One other fish was shown to not engage in spawning activity, and migrated to several areas of the lake during the spawning period. None of these areas were specifically associated with spawning.

Hinch et al. (1996) used EMG radio telemetry to assess the energy utilization of Fraser River sockeye salmon through areas of difficult passage. Their study used the same EMG transmitter and receiver technology used by Kaseloo et al. (1992) and Demers et al. (1996), and the same implant techniques, described by McKinley and Power (1992).

Early Stuart sockeye salmon migrate a long distance upstream to their spawning grounds while fasting, thus likely imposing strong selection for energetic efficiency (Bernatchez and Dodson 1987). Rand and Hinch (1998) developed an energy use model for migrating adult early Stuart sockeye salmon. They simulated total energy use of individual fish during upstream migration using activity measures by EMG radio telemetry. Most energy use models use large time scale estimates, which average energy use over a period of hours or days. However, fish migration involves highly variable activity at fine time scales. Large time scale estimates may not accurately predict energy use by using

mean swim speeds, and may underestimate the use of anaerobic metabolism occurring during short periods of burst swimming. Combining EMG estimates of swim speed with a laboratory model converting swim speeds to energy equivalents, they developed a fine time scale energy use model that accounted for energy use as an exponential function of swim speed. The fine time scale activity measures used by Rand and Hinch (1998) allows more precise and accurate estimates of aerobic and anaerobic energy use and how it affects migratory success.

My first of three objectives is to assess if EMG telemetry can be used to discriminate levels of activity between spawning ground behaviours. Thereby, relative differences in muscle activity could be used for studying behaviour on spawning grounds. My second objective is to compare activity estimates between spawning ground behaviours as spawning progresses, and make inferences as to how muscle activity is used by spawning male and female sockeye salmon. My third objective is to use the activity estimates to generate an estimate of total muscle activity in 'units' of total tail beats by male and female sockeye salmon on the spawning grounds, and use my relative comparison of muscle activity as an 'index' to compare with the actual measures of use of body energy reported by previous researchers on the spawning grounds of the early Stuart sockeye salmon.

METHODS

Study Site Description

The spawning streams of the early Stuart sockeye salmon are the subject of an ongoing fish-forestry interaction study (Steve Macdonald, Department of Fisheries and Oceans, personal communication 1994). The watersheds around several of the spawning streams are designated for logging by different techniques. Thorough studies of these streams are being done both before and after logging to analyze and interpret the impacts of different logging techniques. To further the development of the fish-forestry interaction study I chose to use Gluskie Creek, one of the early Stuart sockeye salmon spawning streams for my study of muscle activity associated with spawning behaviour (Figure 1). I chose this stream for the following reasons:

1. Forestry data loggers record stream temperature 24 hours per day.
2. Easy access exists from a fisheries camp to a pathway along the stream.
3. Grizzly bears, *Ursus arctos*, utilize this stream less often than nearby streams, reducing the chances of conflict.
4. A fish fence operated by the Canadian Department of Fisheries and Oceans in the lower reaches confines the movement of study fish to within the stream, provides samples, and known dates of stream entry.
5. The total fish return for Gluskie Creek is known since 1975.

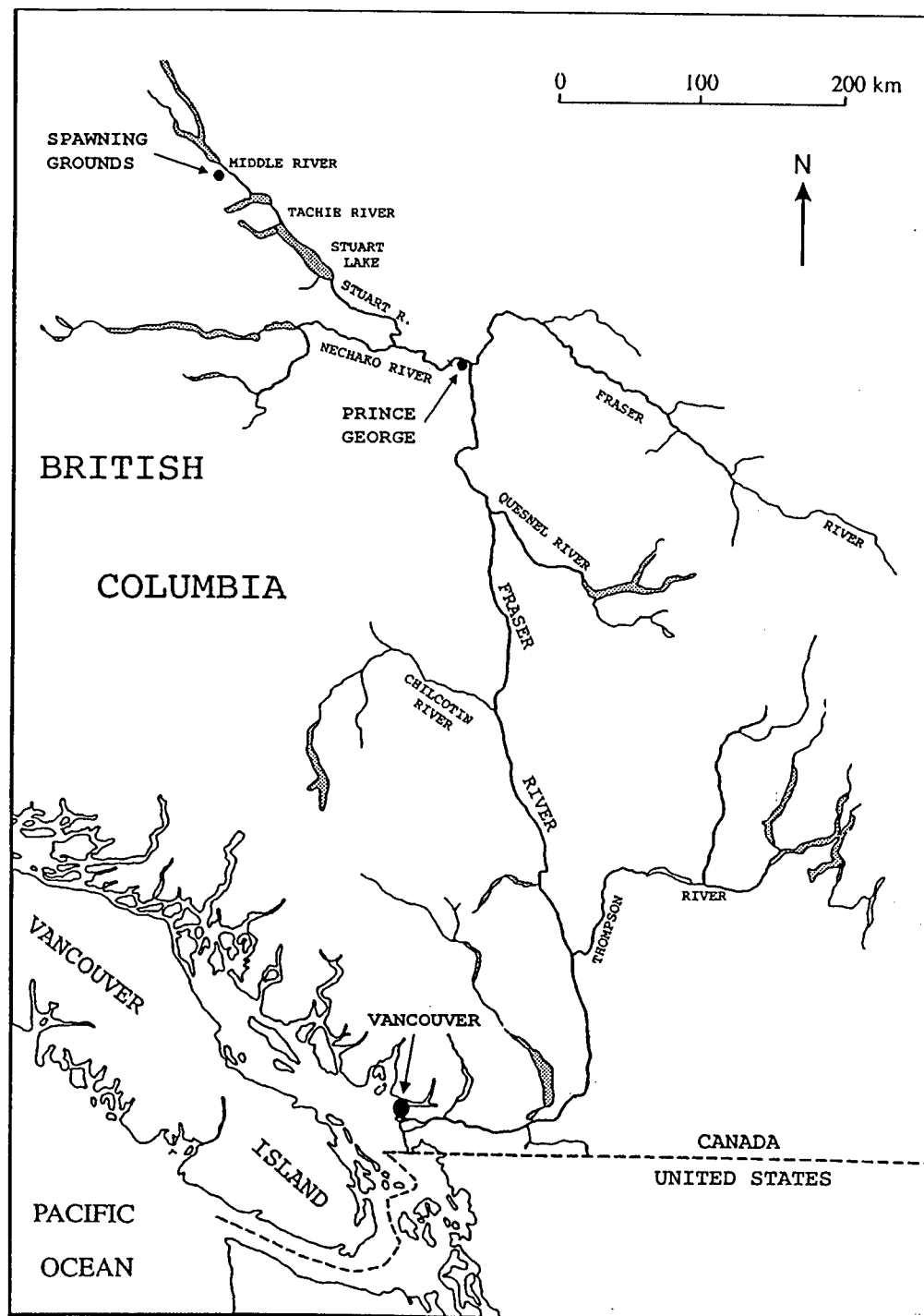


Figure 1: Map of the Fraser River showing the location of early Stuart sockeye salmon spawning grounds and their migration route up the Fraser, Nechako, and Stuart River systems. The Gluskie Creek spawning grounds are indicated on the upper left-hand corner.

Transmitter Implantation

The EMG radio transmitters used in this study are cylindrical, 5 cm long, 1.5 cm diameter, and weigh 20 grams in air. They have two steel wire electrodes, 20 cm long, fitted with 18 carat gold tips 1cm long and 1 mm diameter. A wire antenna, 40 cm long, trails from the radio transmitter's posterior end along with the wire electrodes. Each transmitter has a unique frequency which the radio receiver can selectively detect.

EMG radio telemetry requires the placement of the gold tipped electrodes in the red axial swimming muscle to detect voltage changes associated with the electrical activity of muscle contraction. Both dorsal and ventral axial swimming muscles are used during muscle contractions and all muscles contract simultaneously during spawning (Uematsu et al., 1979). The transmitter's internal electronics detect all voltages over 1-2 μV in amplitude. Voltage signals are multiplied 27,000X, rectified and integrated. Whenever two successive integrated pulses exceeds the predetermined threshold (150 μV) an analogue signal is transmitted to the radio receiver (Lotek model SRX-400). The integrator resets and the process is repeated. By this means, the time interval between EMG pulses is correlated with the frequency of muscle contractions (Hinch et al, 1997). EMG signals are "strongly" negatively correlated with strength and duration of muscle contractions (Sullivan et al., 1963).

Locator radio transmitters also have unique frequencies and are used for tracking and monitoring fish location, and have no electrodes or EMG capability.

These radio transmitters are 4 cm long, 1.5 cm diameter, weigh 15 grams in the air, and have an antenna 35 cm long. They send a radio pulse at regular intervals which is strongest when the receiving antenna is pointed in the direction of the transmitter. Fish carrying either locator or EMG transmitters can be located to within 1 meter of their true location. Tracking requires walking in the direction of the strongest pulse until the fish is found and identified visually.

All fish to be implanted with EMG transmitters were anesthetized using CO₂ generated by a mixture of sodium bicarbonate and glacial acetic acid (method described in Prince et al., 1995). After anesthesia, fish were removed from the anesthetic bath and measured for length (nose-fork), weight, and scale samples were taken. Once the surgery was complete, fish were tagged on their dorsal surface with numbered spaghetti tags for visual identification externally and then released. In 1994, fish were caught on their redds for the surgery and released back on their redds. In 1995, all fish were caught as they arrived at the fish fence. After surgery, fish were released above the fish fence.

The EMG transmitters were surgically implanted by two methods; abdominal implantation (Hinch et al., 1996; Lucas et al., 1993; McKinley and Power, 1992), or subcutaneous implantation which I developed during this study. Abdominal implantation followed methods described in Hinch et al. 1996.

Subcutaneous implantation differs from abdominal implantation in that a horizontal scalpel incision is made just through the skin, about 3 cm long and 5 cm anterior to the pelvic fins. A cannula or other narrow blunt instrument was

used to separate the skin from muscle, opening a 'pocket' 5 cm long anterior to the scalpel incision. The transmitter is pushed through the incision and forced anterior until the incision can be closed. The electrodes are implanted by the same method as for abdominal implantation, but the abdominal cavity was not punctured. Excess electrode wire was tucked under the skin with the transmitter. The antenna is positioned to emerge from the incision in the ventral and posterior direction and does not require cannulation. The pocket was sutured closed with #1 sterile sutures leaving only the antenna wire trailing out. To prevent the transmitter from slipping out if skin sutures fail, the transmitter electrodes may be sutured to the ventral muscle and around the electrodes emerging from the transmitter.

Fish were captured for locator radio transmitter implantation as they arrived at the fish fence. No anesthetic was necessary because this is a quick, relatively non-invasive procedure during which I could hold the fish by one hand in my lap. Each fish was measured for fork length and weight. Locator radio transmitters were implanted down the fish's esophagus into the stomach. Transmitters were first placed at the back of the fish's mouth with the antenna end positioned anterior so the antenna trailed out the mouth. Transmitters were pushed down into the stomach, using the blunt end of a pencil, until the transmitter could no longer be pulled out with a gentle tug on the antenna. The antenna remains trailing out the side of the mouth.

Behaviour Observations

Behavioural observations were made on fish implanted with EMG transmitters, locator transmitters, and fish without transmitters. Once a fish with a transmitter was located for behaviour observations, all fish immediately adjacent to it without transmitters were selected for behaviour observation as well. Each specific behaviour observed is a single observation. An observation period is the total time a fish was observed uninterrupted (i.e. 10 minutes). The maximum upstream movements for each fish with a transmitter were used to compare differences in stream migration between sexes and years.

In 1994 and 1995 sockeye salmon were implanted with EMG radio transmitters, whereas in 1996 locator transmitters were used. In 1994 and 1995, when a fish was located, EMG data were collected with the radio receiver while each behaviour and time of each behaviour was verbally recorded on audio cassette for a 10 minute observation period. This duration of observation was chosen because it allowed all tagged fish and additional fish to be observed within a day, and was the longest duration determined to be repeatable throughout the day without exhausting the observer. In 1995 and 1996, when a fish with a locator or EMG transmitter was located, it was observed for a 10 minute period and all the fish adjacent to it without transmitters were observed for 10 minute periods as well. Behaviours were identified visually and recorded verbally on audio cassette, providing additional records of frequency of each

behaviour in the 10 minute period. Behaviours were timed with a stop-watch in separate observation sets of behaviour duration.

The following behaviour types were observed and recorded: attack, bite, chase, dig, dorsal display, lateral display, quivering, schooling, false spawn, and true spawn. These behaviours were noted during preliminary observations of spawning early Stuart sockeye salmon and are described in Table 1.

Table 1. Behaviours observed and recorded during spawning.

-
1. Attack (charge): fish burst swimming towards and making physical contact with the side of another fish.
 2. Bites: fish grasping and holding the body or fin of another fish, or repeated 'biting' motions on the side of another fish.
 3. Chase: one fish pursuing another fish at variable ranges of speed. The fish rarely makes contact and the subject of the pursuit may accelerate away.
 4. Digs: the fish turns on its side and uses undulations of its tail to disturb the substrate used in redd building by females, and by dominant males as a display in their redd territory.
 5. Dorsal displays: a raising, or fanning out, of the dorsal fin in males. This may occur alone or in combination with other aggressive behaviour, including lateral displays.

Table 1. (Continued)

6. Lateral displays: two male fish swimming side by side with their bodies tilted head up (posturing) at an angle with respect to the water flow. Often accompanied by dorsal displays.
 7. Quivering: high frequency, low amplitude lateral undulations of a male courting a female.
 8. Schooling: newly arrived and relatively inactive fish, often observed 'holding' in pools with other newly arrived fish.
 9. False spawns: the female crouches in the redd as if to deposit eggs, often causing several males to rush into the redd, but no eggs or sperm releases. This typically precedes a true spawn.
 10. True spawn: the female crouching in the redd and releasing eggs with high frequency, low amplitude tail beats. Several males may rush into the redd and release sperm in the same manner.
-

Data Organization and Analysis

EMG pulse interval values which were stored in the data logger, were matched with behaviour observations by associating the recorded time of an EMG pulse interval to the behaviour start and stop time recorded on audio cassette. The clock in the receiver was checked multiple times per day and calibrated to the wrist watch used to observe the time of the behaviour. The EMG pulse interval may occur at any time during the behaviour, therefore the EMG pulse interval records should represent a random sampling of the range of EMG pulse interval values during the behaviour, from initiation of the behaviour to its end. Although subjectivity is involved in associating EMG pulse interval values with behaviour time, these values can be considered random samples of EMG pulse interval values associated with that specific behaviour. Each fish with an EMG transmitter is considered as a single replicate. The same fish when sampled on a different day represents an additional replicate because fish behaviour changes throughout the spawning period.

For each fish, the EMG pulse interval values, which were obtained about every 2 - 5 seconds, were converted to an estimate of $TB\ s^{-1}$ using an equation developed by Hinch and Rand (1998), who empirically assessed $TB\ s^{-1}$ that were associated with a range of EMG values in swimming sockeye salmon. EMG values represent the duration between muscle contractions. Thus, the duration between muscle contractions decreases as the fish increases the rate of muscle contraction, therefore the EMG values are inversely related to muscle contraction

and the tail beat index. $TB\ s^{-1}$ is an index of activity which may be positively correlated with energy expenditure (Weatherley et al., 1996), so EMG values were converted to $TB\ s^{-1}$ to show energy expenditure values in units that increase with energy use. As with EMG values, the $TB\ s^{-1}$ values were generated on a time scale of about 2 - 5 seconds.

Behaviour frequency for all fish was summarized by totaling the number of behaviours occurring each observation period and expressing it as a specific behaviour per minute. This was further summarized by determining means and 95% confidence intervals for TTB, frequency of behaviours, and duration of behaviours using individual fish as the replicates. A skewness test was done to evaluate the extent of skewness. If data were skewed greater than 2.000, they were Log_{10} transformed before conducting statistical analysis. ANOVAs were used to assess differences among behaviour types in rate of $TB\ s^{-1}$, frequency, and duration. Mean TTB required to complete a specific behaviour was determined by multiplying mean $TB\ s^{-1}$ with the mean behaviour duration in seconds. Mean TTB estimated during 10 minute observation periods was determined by multiplying the mean TTB for each specific behaviour by the specific behaviour frequency per minute. The muscle activity expressed in TTB for each behaviour type was determined by determining the mean TTB expended in minutes among replicates for each category and multiplying by the mean longevity of spawning stage, sex, and year.

Ancillary observation was done to determine general spawning behaviour by sockeye salmon in Gluskie Creek, and to determine classifications of fish activity in which to categorize data for more accurate analysis and estimates. The following is an overview of the preliminary observations: Females were fewer than males and would always establish a redd and engage in spawning activity. They would most often hold in a pool with hundreds of other fish during the schooling stage which was used as a status designation. Next they would establish a redd territory and deposit eggs in nests in the stream substrate during the spawning stage. Females with remaining energy would guard their redd until death. Males would often hold in a school and this was used as a status designation for males also. Little or no aggression was observed during the schooling stage among fish of similar or different sex. Males that subsequently established and defended a redd territory during the spawning stage were classified as dominant. Smaller or senescing males that could not establish and defend a redd territory were classified as subdominant. These males typically had little or no access to females. Hence, I classified female status into schooling female, nesting female, and guarding female. I classified male status into schooling male, dominant male, and subdominant male. These behaviour types were used as the class variables for the ANOVAs. A summary of the description of fish used in this study is presented in Table 2.

Table 2. Summary of fish with transmitters used in this study.

<u>YEAR</u>	<u>SEX</u>	<u>WEIGHT(kg)</u>	<u>LENGTH(cm)</u>	<u>METHOD</u>	<u>FREQUENCY</u>
1994	F	2.85	61.5	EMG	150.405
1994	F	2.45	59.2	EMG	150.267
1994	F	2.30	63.1	EMG	150.386
1994	F	1.90	56.8	EMG	150.267
1994	M	4.10	69.7	EMG	150.365
1994	M	3.35	64.5	EMG	151.026
1994	M	3.20	63.5	EMG	150.365
1994	M	2.65	58.8	EMG	150.963
1994	M	2.50	58	EMG	150.023
1994	M	1.15	46.6	EMG	150.885
1995	F	3.50	68.1	EMG	150.424
1995	F	2.30	61.7	EMG	151.064
1995	F	2.25	58.5	EMG	150.862
1995	F	2.25	58.4	EMG	150.682
1995	F	2.15	59.1	EMG	150.345
1995	F	2.15	57.8	EMG	150.105
1995	M	4.15	70.6	EMG	150.245
1995	M	3.75	66.7	EMG	151.124b
1995	M	2.80	60.3	LOCATOR	151.329
1995	M	2.75	60.5	EMG	151.124a
1995	M	2.65	62.5	EMG	150.146
1995	M	2.60	60.1	EMG	150.183
1995	M	2.10	59.6	EMG	150.325
1995	M	2.00	58.4	LOCATOR	151.740
1995	M	1.45	53.5	EMG	150.364
1996	F	3.15	63.5	LOCATOR	151.680
1996	F	2.60	61.5	LOCATOR	151.480
1996	F	2.60	60	LOCATOR	151.230
1996	F	2.40	60	LOCATOR	151.270
1996	F	2.35	60.5	LOCATOR	151.260
1996	F	2.25	58.2	LOCATOR	149.934
1996	F	2.15	58	LOCATOR	151.429
1996	F	1.95	56.5	LOCATOR	151.200
1996	M	4.15	69	LOCATOR	151.540
1996	M	4.15	71.5	LOCATOR	151.380
1996	M	3.80	68.5	LOCATOR	151.410
1996	M	3.75	68.5	LOCATOR	151.659
1996	M	3.50	66	LOCATOR	149.876
1996	M	3.50	67	LOCATOR	151.310
1996	M	3.35	66.5	LOCATOR	151.338
1996	M	3.05	64	LOCATOR	151.440
1996	M	3.00	61.5	LOCATOR	151.740
1996	M	3.00	62	LOCATOR	151.447
1996	M	2.90	62	LOCATOR	149.847
1996	M	2.85	61	LOCATOR	151.239
1996	M	2.65	63.5	LOCATOR	151.280
1996	M	2.45	60	LOCATOR	151.250
1996	M	2.40	60.5	LOCATOR	151.300
1996	M	2.35	60.5	LOCATOR	151.289

RESULTS

Some behaviours chosen for observation were eliminated due to small sample sizes (i.e. false spawns, gamete release), but mean TB s^{-1} was reported. One false spawning sequence followed by a gamete release, and then a chase on an egg predating rainbow trout was observed and matched with corresponding TB s^{-1} values. Because the sample size was small for these types of behaviours, I classified them as "general activity". The sample size (n) and mean TB s^{-1} for the false spawn, gamete release, and chasing the trout, were $n = 10$, mean = 3.3 TB s^{-1} ; $n = 3$, mean = 5.5 TB s^{-1} ; and $n = 5$, mean = 2.3 TB s^{-1} respectively. Gamete release by this female had the highest mean TB s^{-1} of all behaviours.

Some behaviours observed were not included in the analysis. Bites were not often observed. What appeared as bites were a result of locking the jaws with the body of the recipient fish during an attack. No repeated biting motions occurred and the fish appeared to have difficulty separating because of the hooked kype. I observed biting in another Fraser River sockeye salmon population in the lower river. The biting motions were easily discernible and included repeated biting motions on the side of the recipient fish. This behaviour appeared to be biting and added certainty that I did not observe biting behaviour in the early Stuart River population. Circling is not a specific behaviour and can not be attributed to contesting or synchronizing gamete release. Circling may be a single full turn or a half turn followed by a full turn. As circling behaviour

appeared to be a non-specific behaviour, it was left out of the specific behaviour analysis and included as general activity.

Baseline TB s^{-1} were obtained from surgery records of 5 fish under stage 4 anesthesia. The fish were completely immobile and muscle fibers appeared non-tensed. TB s^{-1} data was pooled because there were only 5 data sets. Out of the 5 data sets, 4 were not significantly different. The fifth was examined visually and was not seen as an outlying data set. Therefore I accepted it as a 'normal' variant of baseline data. The TB s^{-1} was 0.694 with a 95% confidence interval of 0.002 TB s^{-1} .

Sample sizes of other behaviour types were quite large therefore, these other behaviours were not "pooled". Estimated number of TB s^{-1} , frequency and duration of behaviour data sets were all positively skewed greater than 2.0 and were therefore \log_{10} transformed before doing ANOVAs. In 1994 and 1995, I collected 10,921 EMG pulse interval records converted to TB s^{-1} that were matched with behaviour observations. Skewness of TB s^{-1} data was 3.979 for all behaviours combined. Skewness after log transformation was 1.591. Behaviours tested with one-way ANOVAs, showed significant effects of behaviour on TB s^{-1} (DF = 20, Error DF = 10900, F = 418, P < 0.001). Mean TB s^{-1} were lowest during the schooling stage and increased when the fish left the school and began spawning (Figure 2). In males, quivers had the lowest mean TB s^{-1} and lateral displays the largest. In females, nest digging had the largest mean TB s^{-1} .

Attacks had a greater mean TB s^{-1} with nesting females than fish of other status. Not all behaviours were observed with females.

Attempts to use the EMG receiver clock to estimate average behaviour duration was abandoned. Most of the behaviours occurred in such short duration (e.g. less than 1 - 2 seconds) as to make estimates with the receiver data very uncertain. Using a stopwatch provided accurate duration with 1/100 second precision. These data were collected in 1996 and applied to all TB s^{-1} data (Figure 3). Applying this method assumes the mean duration did not vary significantly between the years for behaviour. As it applies only to specific behaviours, it may contribute little uncertainty to the estimate of spawning ground TTB by sex and year. For some behaviour duration the sample sizes were small because the frequency of the behaviour was small, so the data were pooled by sex. Measurements of behaviour duration provided $n = 426$ data records. Sample sizes for subdominant males and guarding females were small, but within the range of data collected for dominant males and nesting females. These samples were combined and analyzed by sex, not by status. Skewness was 6.470 for all behaviour duration combined. Skewness after log transformation was 2.606. ANOVAs revealed significant differences in duration of behaviour (DF = 8, Error DF = 417, $F = 55$, $P < 0.001$). Dorsal displays and lateral displays had the longest mean duration (Figure 3). These were behaviours most often observed among dominant males of similar size competing for territory and a female.

Multiplying the mean TB s^{-1} by duration generated an index of mean number of TTB for each behaviour and by status (Figure 4). This describes the mean TTB used for the specific behaviours and allows comparison among specific behaviours using TTB as an index of muscle activity.

Observed frequency of behaviours in 10 minute periods for male and female fish during different status provided $n = 1952$ frequency records for the 6 behaviours observed. Sample sizes provided data for all behaviours during different status. Skewness was 3.592 for all behaviour frequencies combined. Skewness after log transformation was 1.854. A one way ANOVA revealed significant effects of fish status on behaviour frequency ($DF = 5$, Error $DF = 1946$, $F = 79$, $P < 0.001$). Digging was the most frequent behaviour within females, whereas attacks were the most frequent behaviour within males (Figure 5). Digging among subdominant males and guarding females, and quivering by subdominant males were the least frequent behaviours.

In order to evaluate the TTB for each behaviour and status on an hourly time scale, I multiplied TTB (Figure 4) by the corresponding 10 minute behaviour frequency (Figure 5) and then by 6. In Figure 4, TTB values for behaviours of dominant males and nesting females were used where TTB values for subdominant males and guarding females were absent. Because this occurred when frequency of the subdominant male and guarding female behaviours was low, it probably contributed little to the behaviour TTB hr^{-1} (Figure 6). Lateral displays among dominant and subdominant males had the highest mean TTB hr^{-1} . This behaviour

occurred less frequently than many of the other behaviours, but it had a long duration (Figure 3) which contributes to the relatively high value in Figure 6.

I pooled the TTB hr^{-1} of behaviour-specific activity and graphically (visually) compared this to TB hr^{-1} of general activity (Figure 7). The TTB of all specific behaviours among fish of each status contributed much less TTB than general activity during spawning. This was compared between fish of four different status (dominant male, subdominant male, nesting female, and guarding female). Visual comparison of confidence intervals showed differences among the TTB hr^{-1} (specific and general activity pooled) between fish of different status (Figure 7).

Mean TTB hr^{-1} expended during baseline activity, schooling activity, and all spawning activity were compared (Figure 8). Baseline TTB are a large portion of muscle activity in schooling and spawning fish.

One male fish was observed and EMGs recorded during an upstream migration. It traversed pools, glides, and riffles, with riffles most common. Mean muscle activity was 2.13 TB s^{-1} . The migration distance was 326 m. requiring 18.21 minutes of upstream migration; total time for migration was 180 minutes, but this included holding and contesting with other males, and was excluded from the migration time and TTB. Mean swim speed was 111 cm. s^{-1} and ground speed was 30 cm. s^{-1} . The difference is 81 cm. s^{-1} , attributable in part to water velocity. When traversing shallow riffles, the lateral swim muscles were partly out of the water and ventral contact with the substrate was observed.

Spawning ground duration provided $n = 36$ records of total duration. A two way ANOVA was done to test the effect of year and sex on spawning ground duration. Year had no effect on spawning ground duration ($DF = 1$, Error $DF = 32$, $F = 0.440$, $P < 0.512$). Sex had an effect on spawning ground duration ($DF = 1$, $F = 13$, $P < 0.001$). An interaction occurred between year and sex ($DF = 1$, $F = 19$, $P < 0.001$). In 1995, male duration was lower and female duration higher than 1996. In 1996, no difference occurred between male and female duration. This may contribute to the significance of the interaction term and the effect of sex but not year on spawning ground duration (Figure 9).

TTB were summarized by each source of TTB, and by sex and year (Figure 10). Longevity for each status was multiplied by the total equivalent tailbeats hr^{-1} for each status. The constant baseline $TB\ s^{-1}$ was first subtracted from each general activity thereby demonstrating how each activity contributes an increase to the TTB. Baseline TTB were the largest component.

Mean and range of migration upstream of the fence was summarized by sex and year (Figure 11). The data show that the distribution of fish occurred within the lower reaches of the stream which were observed to be high density spawning areas. The position and movement throughout the spawning ground duration of each fish showed a pattern of initial migration followed by association with a specific stream section.

Night observations were difficult because fish appeared to alter their behaviour when exposed to artificial light. Some appeared attracted towards the

light, while others moved away. However, they appeared similarly active at night as during day and were observed to engage in nest digging and contests. More subtle behaviours such as quivering were not observable.

Additional EMG data was collected by allowing the radio receiver to run during various 24 hour periods to compare day and night activity levels. One fish was observed during one 24 hour period and another fish was observed during 5 separate 24 hour periods. Mean day and night activity levels were summarized into 6 hour periods; 2 during day and 2 during night. Some periods were missed when the receiver battery charge was reduced and the receiver shut off. Skewness of data was determined for each 24 hour data set, and the upper range was 3.338, so all data was log transformed. Skewness after log transformation was 1.439. One way ANOVAs revealed significant effects of time periods on TB s^{-1} obtained within the same 24 hour period ($P < 0.001$). Sample sizes were large, preventing analysis of all 6 days of data as a single set. Mean activity levels were compared visually between 24 hour periods and no differences were attributed to diel periodicity (Figure 12). Mean day activity levels and behaviour observations were used as an estimate of mean night activity levels and behaviours. For a senescing male (day 1) and a spawning female (day 2 - 5) differences occurred between 6 hour time periods but did not reveal diel periodicity. On day 6, there was no significant difference ($DF = 1$, Error $DF = 6663$, $F = 0.411$, $P < 0.521$). On this day the female had finished nesting and was beginning redd guarding, thereby changing from nesting female status to guarding

female status. Significant differences occurred within the 24 hour periods in all other days, including the male in day 1. Visual examination of the graph (Figure 12) suggests that fluctuation in $TB\ s^{-1}$ occurred independently of diel periods. No conclusion can be drawn that night activity levels are different than day activity levels.

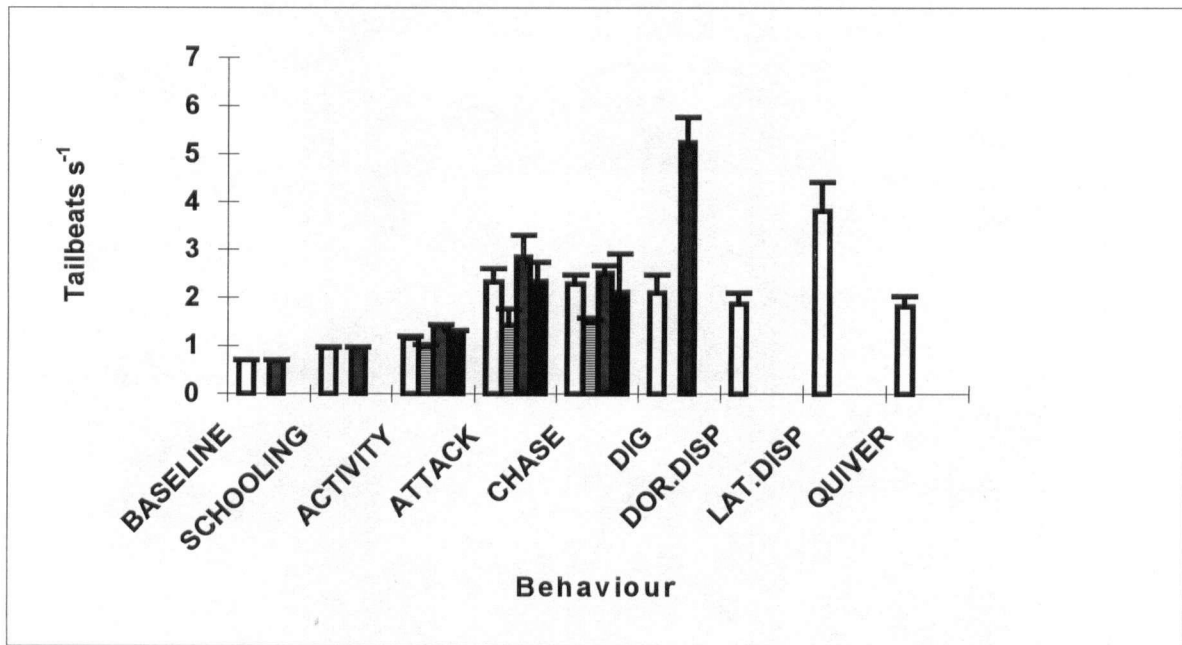


Figure 2: Mean level of activity measured as TBs⁻¹ for specific behaviours compared by fish status. Clear bars, striped bars, spotted bars, and black bars represent dominant males, subdominant males, nesting females, and guarding females respectively. Error bars represent 95% confidence intervals. Baseline and schooling TB s⁻¹ are included in this figure for comparison to specific behaviours and represent males and females respectively. Baseline and Schooling error bars are too small to be seen on this graph. This graph demonstrates the difference between means and 95% confidence intervals between schooling and spawning fish, and between general “activity” and specific behaviours.

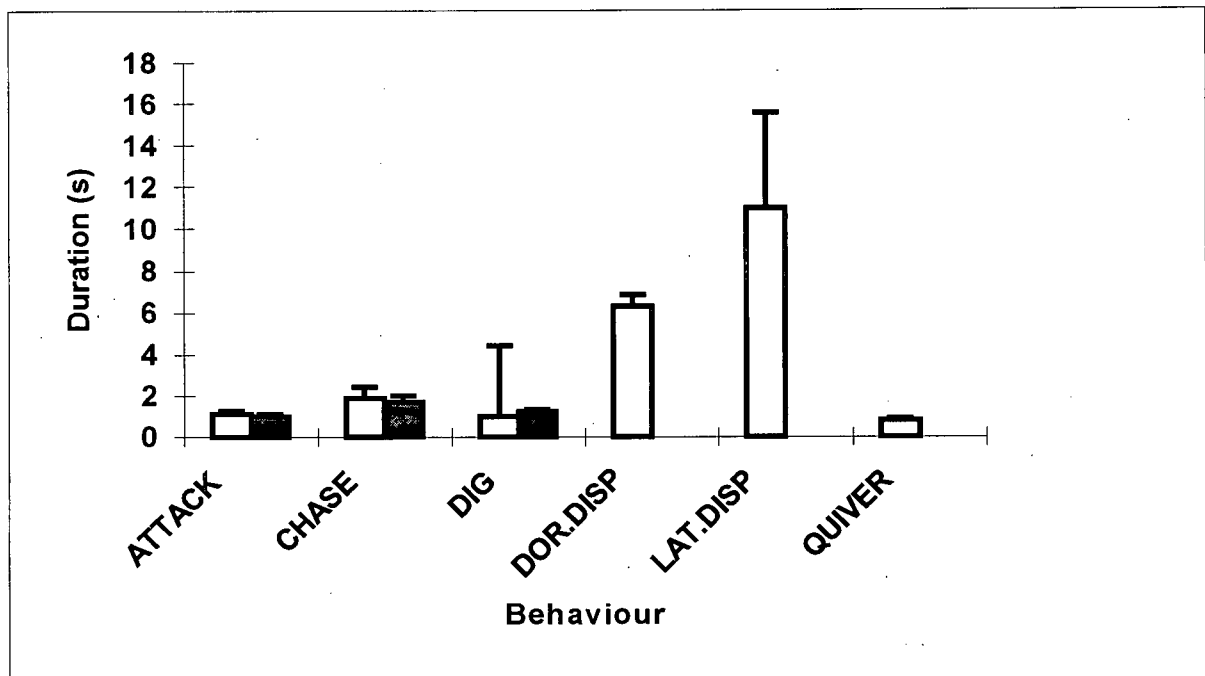


Figure 3: Duration of specific behaviours for males and females. Data for different status within sex were pooled because sample sizes for subdominant males and guarding females were small. Clear bars and spotted bars represent males and females respectively. Error bars represent 95% confidence intervals. Dorsal display, lateral display, and quiver are male displays only.

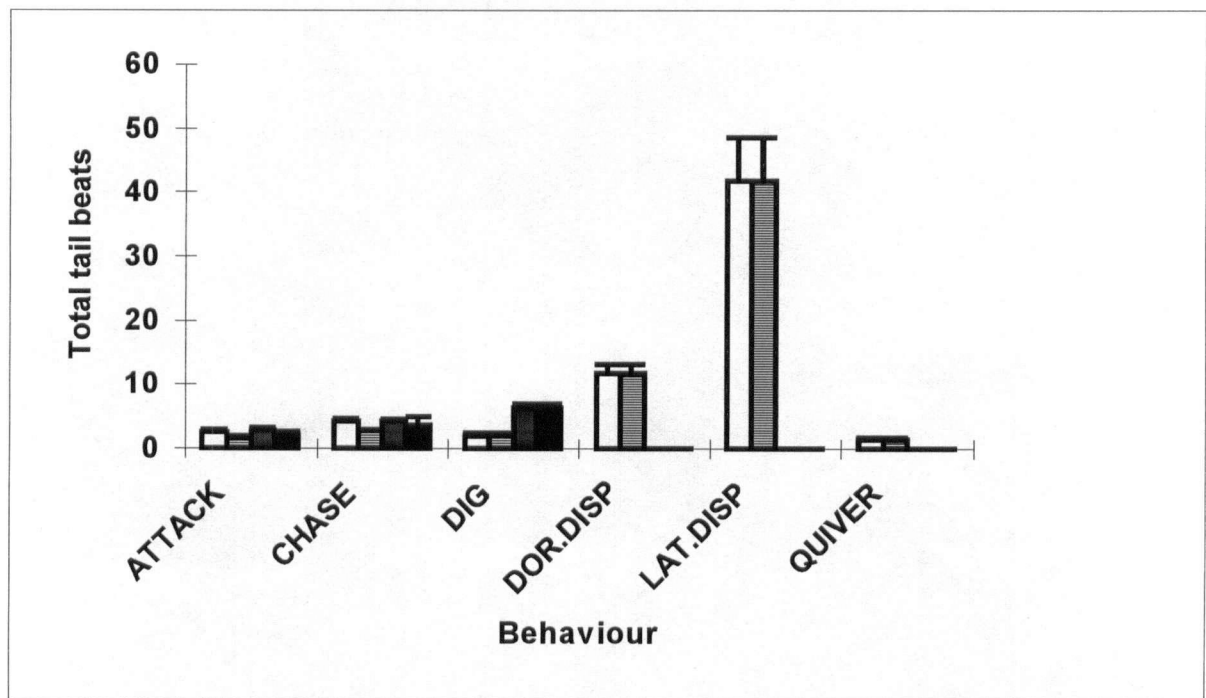


Figure 4: Total tail beats (TTB) for each behaviour by fish status. Clear bars, striped bars, spotted bars, and black bars represent dominant males, subdominant males, nesting females, and guarding females respectively. Confidence intervals represent 95% confidence intervals. Where samples were very small (i.e. 0-1) for subdominant males or guarding females, data from dominant males and nesting females were used as an estimate.

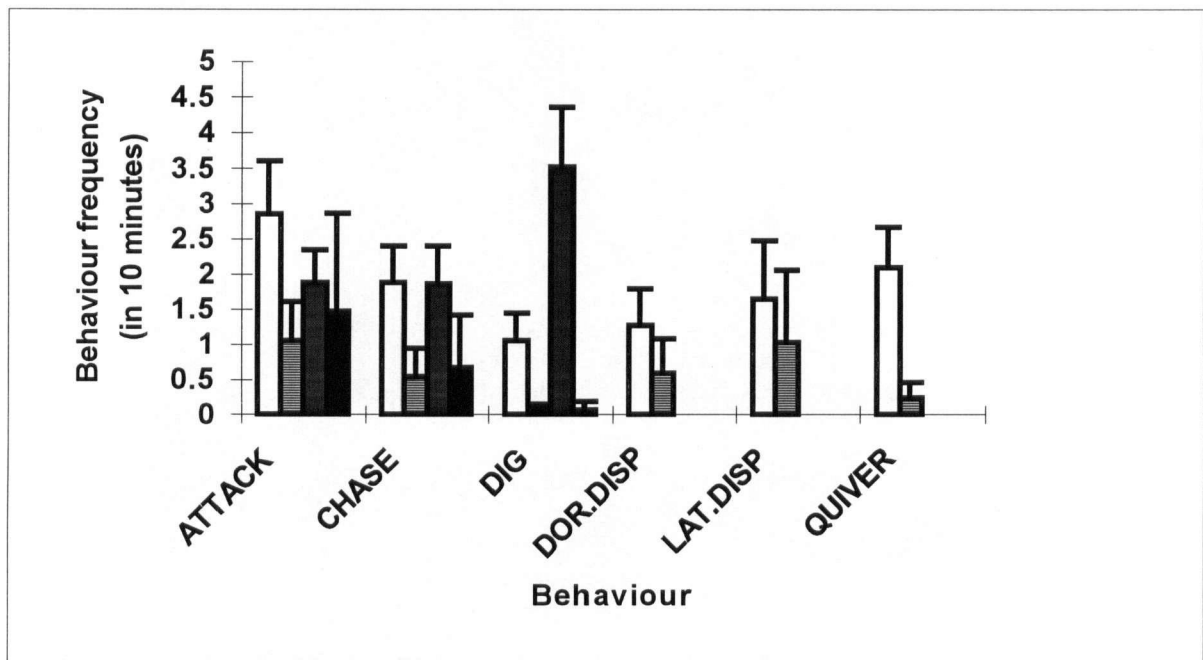


Figure 5: Mean frequency of behaviour occurrence in 10 minute intervals by fish status. Clear bars, striped bars, spotted bars, and black bars represent dominant males, subdominant males, nesting females, and guarding females respectively. Error bars represent 95% confidence intervals.

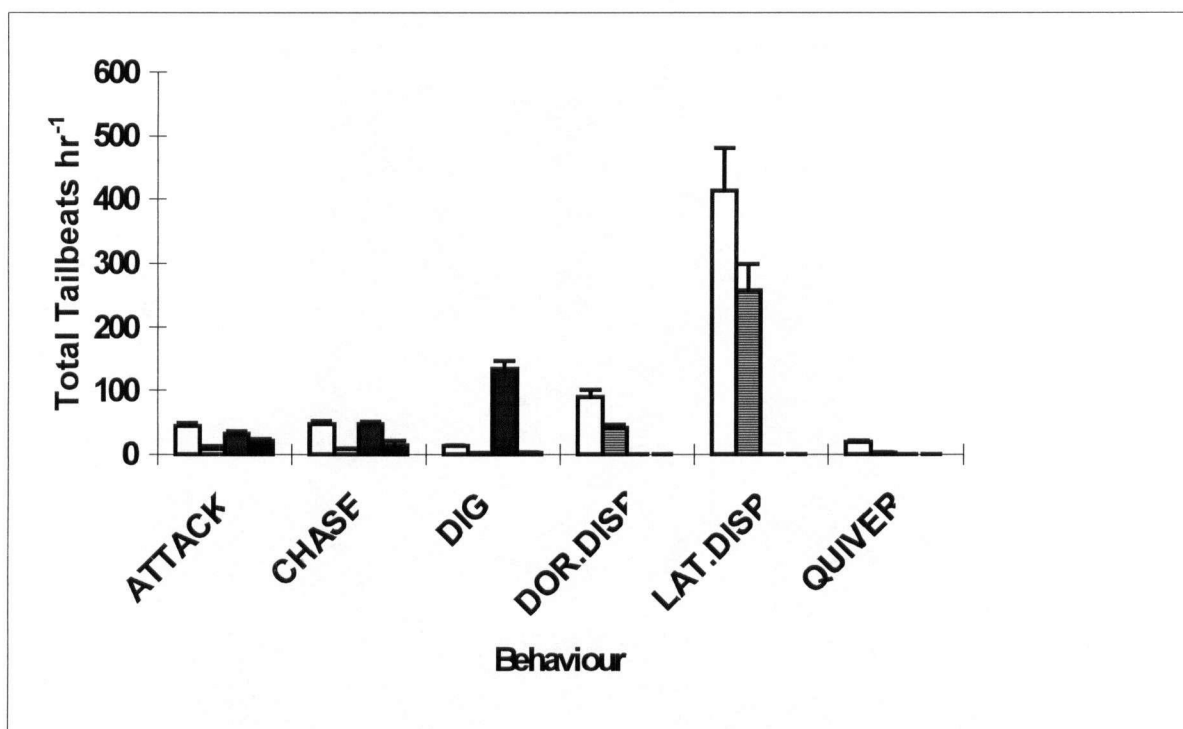


Figure 6: TTB hr⁻¹ for each behaviour by fish status. Clear bars, striped bars, spotted bars, and black bars represent dominant males, subdominant males, nesting females, and guarding females respectively. Error bars represent 95% confidence intervals.

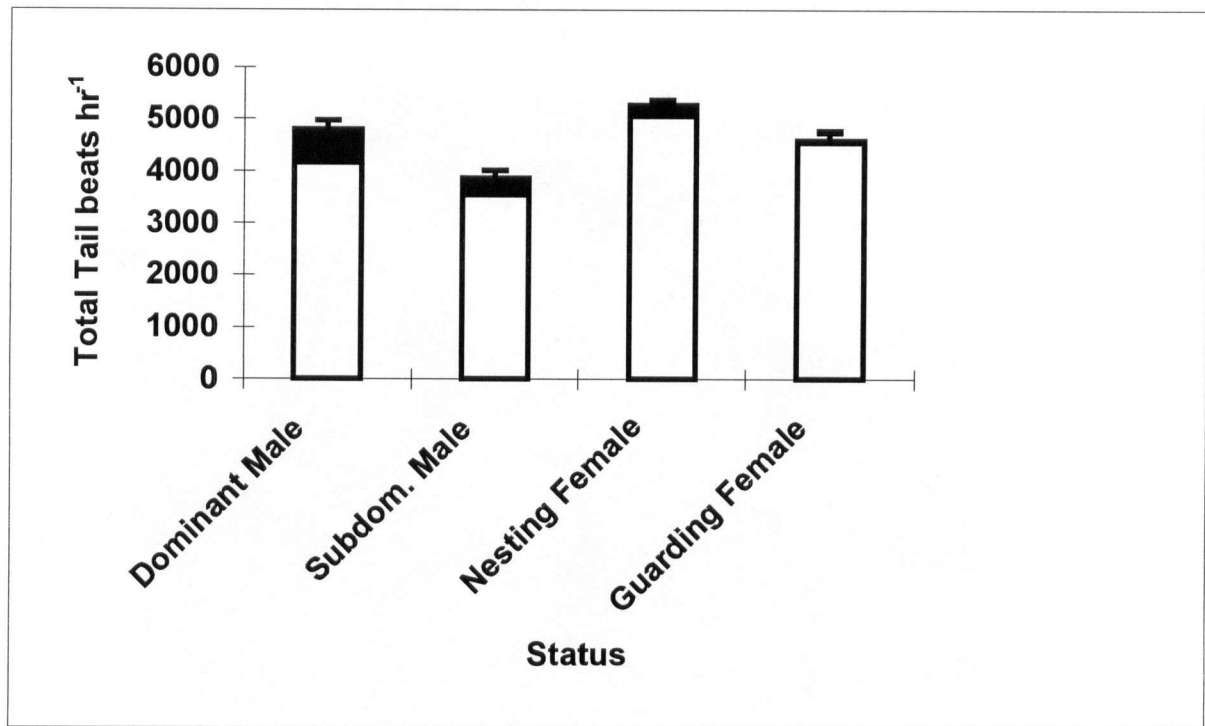


Figure 7: Mean TTB in one hour for spawning fish. Specific behaviours are pooled. Black bars and clear bars represent specific behaviours and general activity respectively. The error bars represent 95% confidence intervals.

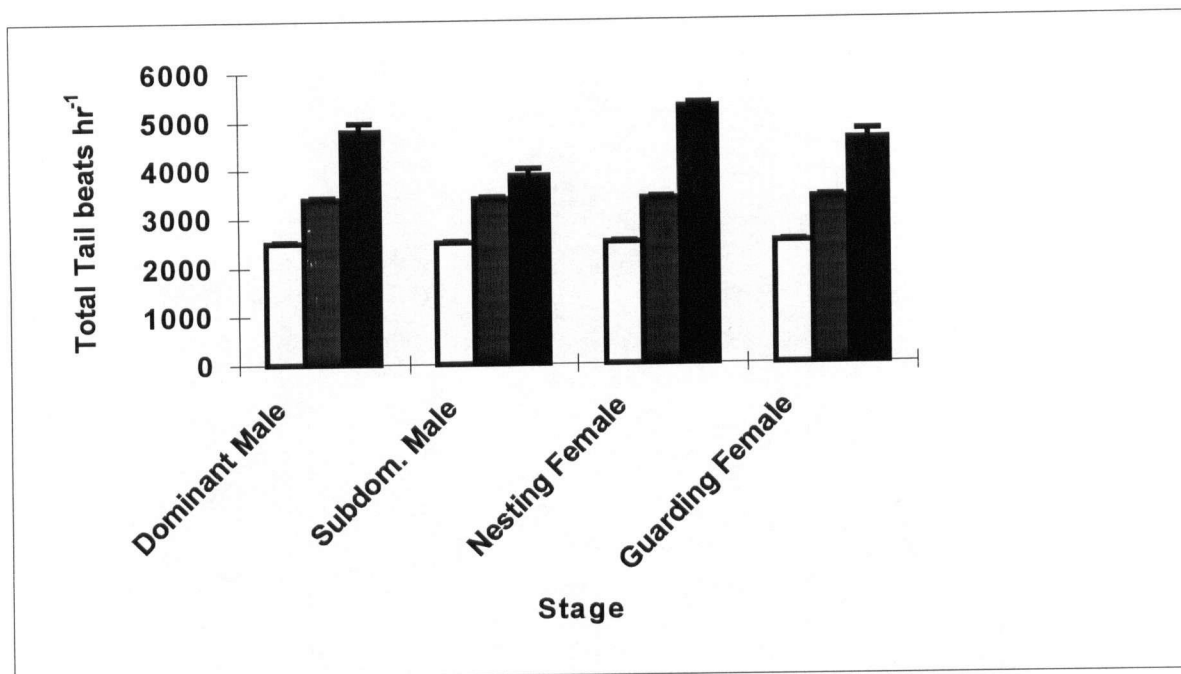


Figure 8: Mean TTB for baseline, schooling, and spawning TTB hr^{-1} . Clear bars, spotted bars, and black bars represent baseline, schooling, and spawning TTB respectively. Error bars represent 95% confidence intervals. Baseline TTB are not deducted from the total schooling and spawning TTB.

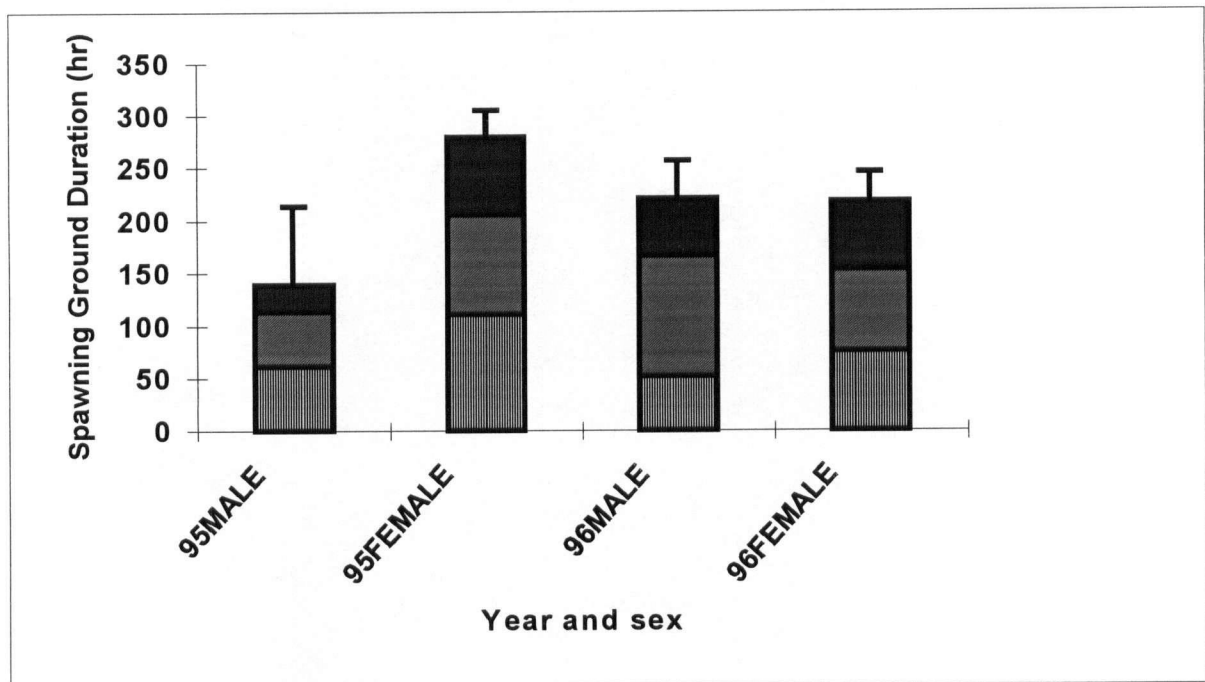


Figure 9: Mean spawning ground duration by sex and year. Vertical bars represent the mean schooling status in both sexes. With males, slanted bars and spotted bars represent the mean time spent as dominant and subdominant status respectively. With females, slanted bars and spotted bars represent the mean time spent as nesting and guarding status respectively. Error bars represent 95% confidence intervals. Females go through schooling, nesting, and guarding in sequential order. Males typically go through schooling, dominance, and subdominance in sequential order.

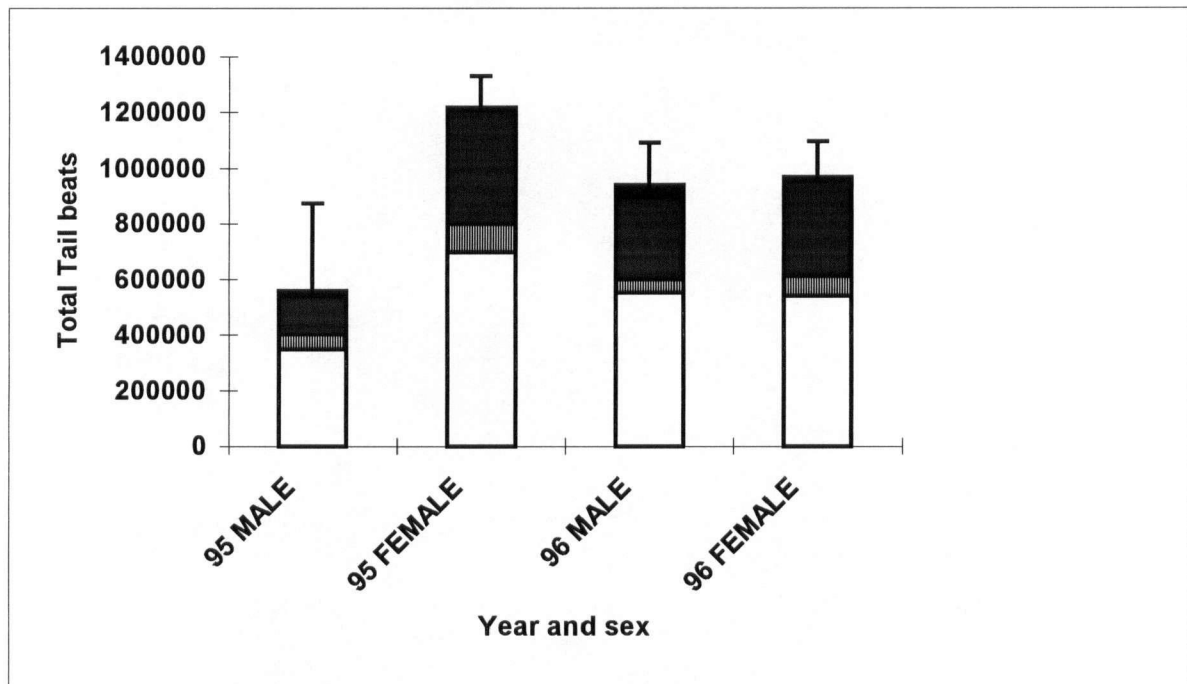


Figure 10: Mean TTB by sex and year. Clear bars, vertical striped bars, spotted bars and black bars represent TTB contribution by baseline, schooling, general activity, and specific behaviours respectively. In stream migration behaviour is included in the graph but is not visible because of its relatively small contribution. Baseline TTB were first deducted from schooling, in stream migration, general activity, and specific behaviours before creating this graph.

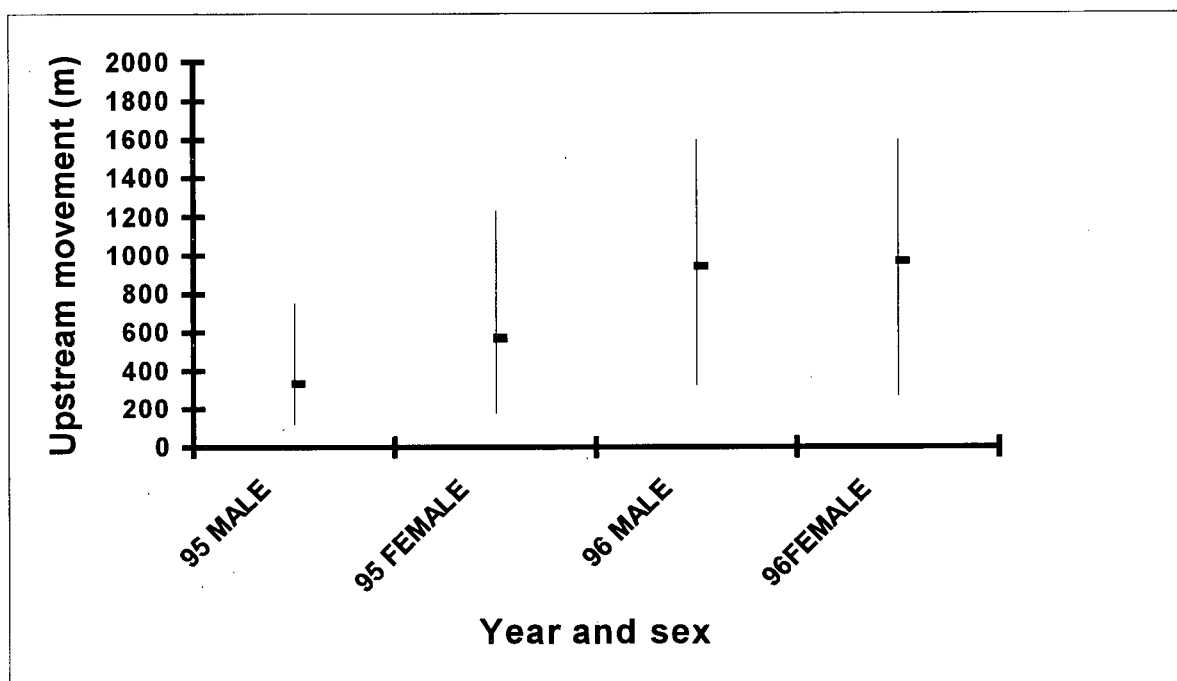


Figure 11: Upstream migration from release point at fish fence by sex and year, showing mean and range.

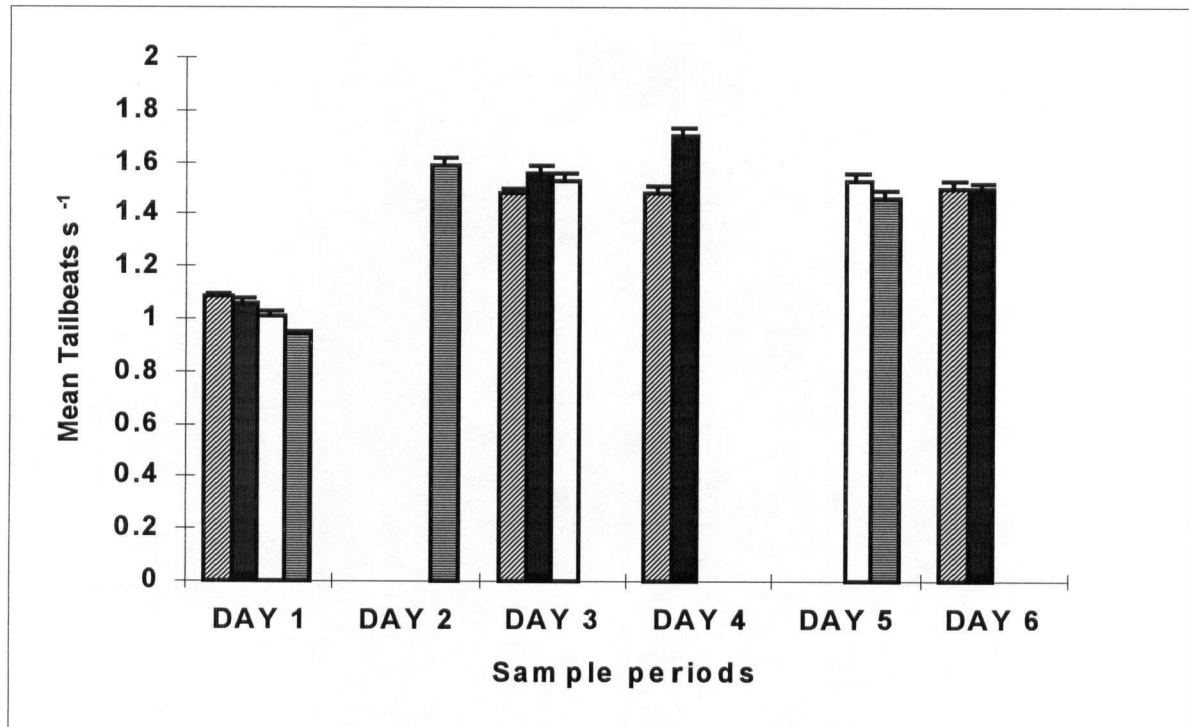


Figure 12: Mean activity levels in 6-hour periods during 6 days of remote monitoring of 2 fish. Nocturnal periods were from 00:00 to 06:00 and 18:00 to 24:00 (slanted and horizontal bars respectively). Daylight periods were from 06:00 to 12:00 and 12:00 to 18:00 (spotted bars and clear bars respectively). Day one represents a dominant male undergoing senescence. Days 2 through 6 represent one nesting female. Redd guarding started on Day 6. Some periods were not recorded if the receiver was used for other purposes or if the receiver malfunctioned.

DISCUSSION

My first objective was to determine if EMG technology could be used to discriminate behaviour-specific activity levels in free ranging sockeye salmon on their spawning grounds. Significant differences were found between the mean activity rate of specific behaviours using EMG. This result demonstrates that EMG telemetry has the precision to discriminate among activity levels at a specific behaviour level. Duration and frequency data, when combined with EMG data, revealed differences in TTB for specific behaviours. EMG technology seems capable of assessing TB s^{-1} and TTB among specific and non-specific behaviours in free ranging sockeye salmon.

My second objective was to compare behaviour-specific activity and general activity among males and females of different status. Behaviour-specific activity was demonstrated to contribute fewer TTB than general activity for fish of all status and sex. Behaviour-specific analysis showed females expend the most TTB in digging nests and is their most frequent behaviour also. The effort required to develop a nest supports that energetically, digging may be the most important specific behaviour for reproductive success in females. The 3 behaviours observed in females were for nest building (digging) and redd defense (attacks and chases).

Territorial males engage in attacks. Attacks have lower TB s^{-1} and duration, but this behaviour has the most frequent occurrence in territorial males.

Attacks by males may not only be for contesting dominance but maintains territorial boundaries and protects access to females. Lateral displays occurred with less frequency but had the highest TB s^{-1} and duration of all behaviours, making this a very intensively active behaviour. It occurs typically between males of similar size. Males of similar size may have to contest more vigorously to establish dominance. Quivering, which is reported by Satou et al. (1991) to provide the male feedback on the females' reproductive state, used the least TTB of all male behaviours. In 5 out of the 6 specific behaviours, males expended the most TTB for territory defense and dominance contests.

There was an effect of status on total mean TB s^{-1} . Dominant males are not significantly different from guarding females, and nesting females have the highest mean specific behaviour TB s^{-1} . Females exhibited 3 out of the 6 behaviours which have a higher mean TTB than the full 6 behaviours used by males. Both females and dominant males dig. Females have a higher TB s^{-1} for digging than males. The higher mean TTB rate of females may be to dislodge substrate in nest building, which male digging does not do.

TB s^{-1} and TTB for specific spawning behaviours were shown to be significantly different for some specific behaviours. TTB expended during specific behaviours demonstrated the important ecological interactions of the fish with its environment from an activity perspective. Behaviour-specific activities may appear to be a large, or largest, source of muscle activity. Comparing hourly TTB from the specific activity to general activity demonstrates that specific

activity contributes relatively little to the TTB. With the exception of baseline metabolism, the majority of TTB used by the fish were in general activity.

In 1995, females had a longer duration on the spawning grounds than males. In 1996, females and males had similar duration on the spawning grounds. The difference in longevity for 1995 males and females may be an effect of total body energy or possibly the males may have engaged in some activity at the mouth of the creek before passing through the fence. Females passing through the fence had no redd territory. All males used for transmitter implants appeared to have arrived 'fresh' with the females. The schooling stage for 1995 males was similar to 1996 males which have significantly greater longevity than 1995 males. The occurrence of schooling behaviour in the 1995 males suggests strongly that they were not already spawning, but freshly arrived.

It was noted that schooling was typical of newly arrived fish, but not for spawning males moving about the spawning stream. All females had their abdomens palpated and assessed for looseness of the eggs from the skeins. In all but one female the eggs appeared partially or entirely in the skeins. The schooling period was longest for females, which may indicate delayed release of eggs from the skeins until arrival at the spawning grounds. The schooling period may allow the eggs to release from the skeins into the abdomen while expending the least energy via muscle activity before the female proceeds onto the riffles to establish a redd territory. Schooling uses fewer TTB than spawning, suggesting that when schooling occurs, reduction in TTB expenditure may be adaptive.

Females arriving with eggs still retained in the skeins may school to save energy while the eggs mature and release from the skeins.

One female that had eggs already released from the skeins upon arrival at the fish fence proceeded immediately to establish a redd territory, bypassing schooling. This female was the shortest lived and just finished nesting, without time left for redd guarding, before death. The observation of this small female arriving with eggs already released in the abdomen, suggests that females arriving late with little energy left may begin to release eggs from their skeins before they arrive. This would allow them to avoid expending available energy by not schooling. Partial spawns or pre-spawn mortalities may result if available energy is insufficient to complete spawning. Delaying the release of eggs from skeins until reaching the spawning grounds may be adaptive only if available energy stores allow extra time schooling. The skeins may protect the eggs from infection, water hardening, and loss out the vent during a burst swim. The retention of the eggs in the skeins may also effect the centre of gravity, and subsequently the swimming efficiency of the fish.

Baseline activity was determined from fish in stage 4 anesthesia. This may approximate basal metabolism for lateral swim muscles. This assumes that baseline $TB\ s^{-1}$ are a measure of involuntary random contraction of muscle fibres. Other metabolic processes in these anesthetized non-feeding fish may contribute little energy use. The term 'baseline' metabolism rather than basal metabolism is used to avoid making untested assumptions about the effects of CO_2 anesthetic on

metabolic processes of fish. Baseline activity contributed much of the TTB. If baseline TTB are subtracted from schooling and spawning activity, the contribution of schooling TTB and spawning TTB to total muscle activity is shown to be far less than the absolute measurement during these activities. This suggests from an energetic perspective that remaining inactive for part of the day is not a good spawning strategy unless the fish is not yet ready to spawn.

Two fish were observed for patterns of diel fluctuation in TTB expenditure. The females TTB use may fluctuate more in association with cycles of egg releases, and subsequent rapid nest backfilling. However, data are insufficient to determine the cause of any fluctuation. The lack of a detectable pattern may indicate TTB expenditure is similar during day and night. Spawning, specifically the more obvious behaviours, were observable at night. But less obvious behaviour was not easily observed, so night observation was not able to be done accurately. Due to the similarity of day and night TTB expenditure, I chose the assumption that diel activity was the same regardless of light levels. Coho salmon spawn at low densities, and most often at night thereby reducing predation (Prince 1997). Sockeye salmon spawn in high densities typical of a 'flocking strategy' (Roff 1992) and may thereby reduce their individual chance of being selected by a predator. Early Stuart sockeye salmon have large energy constraints due to their long migration. They may not have sufficient energy for diel periods of spawning activity and must use an 'all out' spawning strategy because $TB\ s^{-1}$ occur even when they are inactive. Schooling fish are inactive day

and night, but this may be adaptive for reducing $TB\ s^{-1}$ while eggs mature, as explained previously.

Mean temperatures varied little during the years 1995 and 1996. Brett (1995) found temperature increases the maximum sustainable activity rate more than increasing metabolic demand during activity, and this effect is small for temperatures between 5 to 10°C. Any temperature effects may be corrected in part by the methodology used in this study (i.e. EMG radio telemetry)(Hinch and Rand 1998). If a significant temperature effect occurred it would not alter comparisons of total muscle activity in the same year. Therefore, a relative comparison between sexes is valid within each year. Comparing the muscle activity of the same sex between years may have additional error due to temperature effects. However, this error may not be significant because the differences in sexes between years is large and the differences between mean temperatures are small.

My third objective was to use the activity measures to derive an estimate of TTB, and compare the relative amount of activity by sex and year to the results reported by Idler and Clemens (1959) and Gilhousen (1980). Gilhousen (1980) in a re-analysis of Idler and Clemens (1959) data, reported male sockeye salmon utilize more energy than females in the early Stuart population. My data shows two alternative results in comparing muscle activity. I found that males utilized less TTB and had shorter spawning ground duration in 1995, and males were equal to females in TTB and spawning ground duration in 1996. Idler and

Clemens (1959) used body constituent analysis to determine kilocalories utilized, whereas I used muscle activity (TTB) to compare energy use. Although the units of energy are different, comparative analysis is still appropriate. Gilhousen (1980) showed the males had more constituent energy upon death than females, but utilized more kcal/kg/day. My data show the females used more TTB day⁻¹ during the spawning stage. However, if the females hold in schools for a longer duration, this may lower their total mean spawning ground activity rate in years where spawning ground duration of females is equal or greater than males. Unlike Idler and Clemens (1959), I assessed how energy is used during different stages of spawning. Differences in male and female longevity and TTB expended by status may effect total energy used by sex and year. Gilhousen (1980) showed that male sockeye salmon used more energy than females in both years reported by Idler and Clemens (1959). Two possible alternatives could have been found. The females could have used more energy, or both sexes could have used the same amount of energy. My data for two years showed both alternatives. In 1995 the females used significantly more TTB, and in 1996 both sexes used the same TTB. This suggests that either alternative is possible and Idler and Clemens' (1959) data do not define a 'rule' of energy use with male and female early Stuart sockeye salmon. Idler and Clemens (1959) sampled newly arrived fish on the spawning grounds and then 'fresh' dead fish. This method requires many assumptions about energy use by different fish and does not sample the same fish 'before and after'. My study had the improvement of following specific

fish from arrival until death. This provided detailed analysis of effects of behaviour, status, and individual fish duration on the spawning grounds on TTB expenditure.

In summary: following the procedures to test my first objective, I used EMG measurements of lateral swim muscle contractions to discriminate muscle activity in $TB\ s^{-1}$ and in TTB units for specific behaviours. This shows EMG technology has the precision required to measure muscle activity associated with specific behaviours. Measures of $TB\ s^{-1}$ and TTB for specific behaviours may allow a more insightful analysis of the ecological significance of the behaviour. Following the procedures to test my second objective, mean TTB were compared for behaviour-specific behaviours and general activity (and by status, sex, and year). Specific behaviours, which have a higher $TB\ s^{-1}$ than general activity, were shown to contribute the least to TTB of the fish during its life on the spawning grounds. This suggests general activity is the largest source of activity and subsequently energy expenditure in spawning sockeye salmon. My third objective was difficult to test because I was comparing TTB to kilocalories consumed. I used a relative activity approach to compare TTB, whereas Gilhousen (1980) used an absolute measure of energy in kilocalories. However, I suggest that when comparing similar techniques first, comparisons may be made among the conclusions by the two different techniques. Therefore I suggest the comparison of my data to Gilhousen's (1980) data allows an inference to be made between the studies. TTB use by sex in both study years was different than kilocalorie

results reported by Gilhousen (1980). Gilhousen's (1980) results could be influenced by unstated assumptions about the duration of males and females on the spawning grounds. Differences may occur between sexes and years in somatic energy storage and expenditure.

In conclusion, EMG radio telemetry is an effective method of measuring muscle activity and comparing energy expenditure. It may, with calibration, provide a direct estimate of energy expenditure in spawning fish.

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APPENDICES

APPENDIX I

DEFINITION OF TERMS

Pacific Salmon Names:

Oncorhynchus - Pacific salmon genus [Latin; hooked nose]

gorbuscha - pink salmon [Russian; hill, hump salmon]

keta - chum salmon [Russian; China, Chinese salmon]

kisutch - coho salmon [Russian; swarming, darting salmon]

nerka - sockeye salmon [Russian; schooling, fearless salmon]

tshawytscha - chinook salmon [Russian; longest, largest salmon]

Definition of Terms:

charr - a salmonid [Scottish; from Latin 'char' - to change color]

diel - a full 24 hour day [Latin; 'dies' - a completed cycle]

diurnal - by day [Latin; 'diurn' - day]

esophageal - through the esophagus, placing a transmitter in the stomach.

nocturnal - by night [Latin; 'nocturn' - night]

redd - area of nest digging [Scottish; - clear]

salmo - trout genus [Latin; salmon, salmo, 'salio' - to leap]

salvelinus - charr genus [Latin; 'salve', 'linus' - healthful type]

skeins - 2 membranes containing egg follicles which mature into eggs.

subcutaneous - under the skin.

trout - a salmonid [Latin; trutta, from Greek troktes, 'trogos' - to gnaw]

APPENDIX II

FISH ESCAPEMENT TO GLUSKIE CREEK

Fish Escapement by Year and Stream.

<u>YEAR</u>	<u>GLUSKIE</u> ¹	<u>FORFAR</u>	<u>O'NE-ELL</u>
1975	10370	9818	25124
1976	966	1249	6727
1977	4646	3628	5893
1978	4295	9579	10649
1979	10040	15805	34228
1980	1049	2328	10661
1981	10741	12228	13452
1982	452	17975	1170
1983	3781	13073	7822
1984	6943	2221	16933
1985	17381	9922	20347
1986	3468	5455	7000
1987	19973	23395	41424
1988	17700	24640	53447
1989	9062	10824	22528
1990	12078	14994	21243
1991	17365	21885	28489
1992	3749	12904	11002
1993	30052	37700	38046
1994	3919	4902	4371
1995	9500		
1996	8000		

¹ Gluskie Creek was the study stream.

Two adjacent creeks are shown for comparison.